JOURNAL OF ANIMAL BEHAVIOR

VOL. 4 MAY-JUNE, 1914 No. 3

CONSPICUOUS FLOWERS RARELY VISITED BY INSECTS[1]

JOHN H. LOVELL,
Waldoboro, Maine

There are many cultivated flowers adapted to winged pollinators, which are rarely visited by insects although they are of large size and display the most brilliant hues. Among the species enumerated by Plateau as illustrations are the red geranium (*Pelargonium zonale* Willd., hybrid Lepidopterid flowers from Southern Africa), the scarlet sage (*Salvia splendens* Sellow, ornithophilous, from Brazil), the cardinal flower (*Lobelia cardinalis* L., ornithophilous, from North America), and the splendid gaudy flowers of *Passiflora incarnata* L. (probably ornithophilous,[2] from North America).[3] Other neglected flowers employed by Plateau for experimental purposes were *Lilium candidum* L. (hawk-moth flowers), *Passiflora adenophylla* Masters (?), (probably a hybrid), *Œnothera speciosa* Nutt. (hawk-moth flowers), *Pisum sativum* L. (almost invariably self-fertilized, probably introduced from Western Asia into Europe in prehistoric times),[4] *Pelargonium zonale* Willd., *Clematis Jackmanni* Jack. (hybrid pollen flowers), and *Petunia hybrida* Hortul. (hybrid, the South American species are ornithophilous?). That anthophilous birds and insects have played an important part as pollinators in the phylogenetic history of the flowers enumerated, in the

[1] The pollination of green or inconspicuous flowers has been considered by the writer in an earlier paper. *Am. Nat.*, **46**:83–107, 1912.

[2] In Alabama Trelease saw the flowers visited by humming-birds. Knuth, Paul, "*Blütenbiologie*," **3**: 510.

[3] Plateau, F., "Les insectes et la couleur des fleurs," *L'Année Psychologique*, **13**:72.

[4] De Candolle, A., "Origin of Cultivated Plants," p. 329.

lands where they are or were endemic, will not be questioned by any orthodox floroecologist. But manifestly when they are cultivated in widely separated stations, under the most diverse conditions, there is a strong probability that in many localities their normal pollinators will be entirely absent or extremely rare; while the flowers themselves modified both in form and function by artificial selection and hybridization may cease to remain equally attractive, e.g., double flowers may be devoid of both nectar and pollen. On the other hand why should we expect common Hymenoptera and Diptera frequently to visit flowers from which they can not legitimately obtain nectar, and to which they are not beneficial; or why should we look for diurnal insects as common visitors to crepuscular flowers ? One of the advantages of reciprocal adaptation between flowers and their pollinators is the exclusion of injurious and useless forms.

But Plateau assumes that all bright-hued flowers, according to the theories of Müller and Knuth, no matter what their manner of pollination, should frequently be visited by diurnal insects. The rarity of insect visitors to many beautiful flowers with very showy colors, he remarks, places the biologists of the school of Hermann Müller in a singularly embarrassing position.[5]

He summarizes his views as follows:

" My observations establish the truth of the fact, well-known though not sufficiently insisted upon, of the existence of many plants with flowers formed on the entomophilous type and presenting large dimensions as well as brilliant colors, which attract almost no diurnal insects.

It follows that the attractive rôle, or, as it is often called, vexillary rôle of the forms and colors of floral envelopes is either nul or of very little importance.

Causes of attraction other than colored surfaces are necessary to bring pollinators to flowers and to lead them to return again after a first visit; they are an odor, which is agreeable to the insects, and a sweet liquid, which permits them to appease their hunger and provide food for their young.[6]

Unfortunately for the general acceptance of Plateau's conclusions, they are not of universal application, but are controverted

[5] Plateau, F., " Recherches expérimentales sur les fleurs entomophiles peu visitées par les insectes rendues attractives au moyen de liquides sucrés odorants," *Mem. de l'Acad. roy. de Belgique*, 2me sér., 2:5, 1910.

[6] *Loc. cit.*, pp. 51–2.

by the characters of various natural flowers. The cornflower, (*Centaurea Cyanus* L.), *Gentiana acaulis* L., and several other gentians have conspicuous nectariferous flowers, which are visited by numerous insects although they are devoid of scent. Bees frequently gather pollen from poppy flowers, which are not only nectarless but possess a faint unpleasant odor. From the wind-pollinated, purple flowers of the elm, which are both nectarless and odorless, honey-bees in immense numbers sometimes procure pollen for early brood-rearing; while many other anemophilous species are also valuable to the bee-keeper as sources of pollen. Nor is it stated that there are many conspicuous flowers, which are neglected by insects notwithstanding they are strongly odoriferous, as the sweet pea, *Lilium candidum*, and varieties of *Pelargonium*, which have the entire plant pleasantly scented. Finally, if a flower is rich in nectar, it may be both inconspicuous and odorless and yet receive numerous visits. According to Fritz Müller, there is in South Brazil a species of *Trianosperma* which is visited very abundantly all day long by *Apis mellifera* and species of *Melipona*, although the flowers are scentless, greenish and to a great extent hidden by the foliage.[7] It is thus apparent that the visits of insects in large numbers are not dependent on the presence of an agreeable odor.

But, assuming the validity of his conclusion that bright coloration is without significance because certain conspicuous flowers are commonly neglected by insects, Plateau performed a long series of experiments, in some instances introducing honey and in others odoriferous sweet syrups into neglected flowers with the result that in most cases insects were attracted, often in large numbers. In his earlier experiments of 1897, he employed only honey diluted with water. When a small quantity of this mixture was placed on the handsome flowers of *Pelargonium zonale, Phlox paniculata* and *Anemone japonica*, it was speedily discovered by numerous Diptera and Hymenoptera. Similar results were obtained with greenish or dull-colored flowers. The vexillary organs are, therefore, asserted to be of little or no importance.[8]

Knuth considered these experiments of no value since " they

---

[7] Müller, H., " Fertilization of Flowers," p. 270.

[8] Plateau, F., "Comment les fleurs attirent les insectes," 3me part., *Bull. de l'Acad. roy. de Belgique*, **33**:27–37, 1897; 4me part., loc. cit., **34**:604–10, 1897.

only prove that the odor of honey exercises a great power of attraction which has long been known. It is only necessary to place honey anywhere to secure the immediate appearance of numerous insects which are fond of it."[9] To this criticism, Plateau replied:

"Quelle pauvre argumentation! Knuth ne s'aperçoit pas qu'il me donne pleinement raison. En effet, s'il a suffi de l'introduction d'un peu de miel dans des fleurs habituellement négligées pour y amener les Insectes, c'est que l'éclat des corolles ne compte guère et que le perfum de la substance que ces animaux recherchent avidement a constitué seul l'excitant déterminant leurs actes. J'avais donc démontré ce que je voulais démontrer."[10]

Plateau's conclusion that certain conspicuous flowers, which are devoid of nectar and pollen, or nearly so, are neglected because insects fail to notice their colors, it is believed, can readily be shown to be fallacious. The flowers are neglected not because they escape attention, but because anthophilous insects have learned from experience their inability to procure food materials from them. They do not neglect them entirely, but visit them occasionally,[11] although they do not often repeat their futile visits since "memory appears to replace both odor and color as the directive stimulus of first importance.[12] In his experiments with odoriferous essences, that is, odors without a sweet syrup, Plateau recognized the fact that if they are employed alone a Hymenopteron or Dipteron entering the corolla and finding nothing will not return again.[13] This statement is

---

[9] Knuth, Paul, "Handbook of Flower Pollination," translated by J. Ainsworth Davis, 1:206.

[10] Plateau, F., "Recherches expérimentales sur les fleurs entomophiles," etc., p. 8.

[11] This statement will be supported later by a large number of observations.

[12] Coulter, Barnes and Cowles, "Textbook of Botany," 2 (Ecology by H. C. Cowles) :850. On the memory of honey-bees cf. Forel, A., "Ants and Some Other Insects," translated by W. M. Wheeler, p. 28; and on the memory of place in bees cf. Buttel-Reepen, H. V., "Are Bees Reflex Machines," translated by M. H. Geisler, pp. 19–39. In the autumn of 1912 I placed a dish containing fragments of comb honey in a secluded spot nearly surrounded by a steep bank and willow bushes. A few bees were brought to the honey and it was soon visited by a large number. After they had been fed several times the dish was removed and everything left as at first. Two weeks later I examined the place but failed to discover a single bee. The weather was, moreover, growing colder and they were no longer flying freely. I now placed on the same spot as previously another dish of comb honey; and two hours afterwards I found it swarming with bees. During two weeks they had evidently kept this locality under constant surveillance, inspecting it from time to time, although there was nothing to attract their attention.

[13] Plateau, F., "Recherches expérimentales," etc., p. 10.

equally applicable to color. Neither color nor odor separately or together will attract insects continuously, if they can obtain no spoil.

Plateau was equally mistaken in supposing that the addition of an agreeable odor is indispensable; for it is only necessary to introduce a solution of sugar and water, which is odorless, to bring insects to the flowers in great numbers, as will be shown experimentally. In the absence of accessible food materials pleasantly scented flowers will not be visited more frequently than would be the case if they possessed only bright coloration. Insects will not repeatedly visit an inflorescence because they experience an aesthetic pleasure. This is well shown by *Lathyrus odoratus* L., or the sweet pea, which, notwithstanding its strong fragrance and brilliant hues, is very rarely sought by insects, because the nectar is inaccessible to nearly all of them. An ample, available food supply will alone secure continued and frequent visits of insects to flowers. Since it can be shown, therefore, that an inflorescence can be rendered very attractive to insects without the addition of an odor, it logically follows from Plateau's own method of reasoning that conspicuousness is beneficial.

When Plateau introduced honey into certain selected flowers, they received two allurements, an agreeable odor and a sweet liquid food, which sharply distinguished them from the flowers left in their natural state. In effect, the flowers containing honey became distinct physiological varieties. Color and odor were not brought, therefore, into competition on equal terms; the flowers in their natural state possessed only color and form, while those into which honey was introduced possessed color, form, an agreeable odor and a liquid food. Manifestly, the latter flowers were given the greater advantage, and it is unfair to conclude that because they received the greater number of visits, odor was essential and color was of no significance. Throughout Plateau's experiments, the presence of the vexillary organs was a source of error. As he had assumed that they were of no value, it is difficult to understand why he did not remove the floral envelopes, when the flowers would of necessity have been compelled to depend wholly on the odoriferous liquid food. Finally, to have made the competition impartial, an odor-

less syrup should have been introduced into the empty flowers. The experiments were, therefore, not well adapted for the purpose intended and the results obtained, as interpreted by Plateau, are misleading.

In another series of experiments, Plateau unsuccessfully attempted to draw insects to flowers by means of the odoriferous essences of lavender, thyme, sage, and mint. "The Labiatae are habitually much visited by bees and I hoped in giving the preference to essences extracted from these plants to see bees and allied insects drawn to the flowers." Essences of orange and bergamot were also employed. But the attraction proved very small or non-existent. Certain essences as thyme and sage were feebly attractive, while mint was even repellent.[14]

Knuth makes the following comment: "From these experiments it follows that solutions of odoriferous plant extracts, which ought to attract insects, do not do so."[15] Plateau subsequently attributed the failure of the flowers to attract insects to the too violent and medicinal odors of the extracts employed; they never possessed the delicate perfume of the plants from which they were extracted. In a new series of experiments undertaken in the spring and summer months of the years 1907-9, instead of odoriferous essences, odoriferous liquid foods, which it had been previously ascertained were attractive to insects, were introduced into neglected flowers. The sweet liquids employed were anisette[16] (essence of anise, syrup of sugar and diluted alcohol), the cooked juice of cherries, syrup of cassonade[17] (syrup of brown sugar to which a few drops of rum had been added), and syrup of Angelica[18] (syrup of cane sugar flavored with a strong aromatic essence obtained from the petioles of *Angelica officinalis*). Fifty-five experiments were performed with these syrups, but descriptions of only a part of them were published, those being selected

---

[14] Plateau, F., "Comment les fleurs attirent les insectes," 5me part., *Bull. de l'Acad. roy. de Belgique*, **34**:872–5, 1897.

[15] Knuth, P., "Handbook of Flower Pollination," **1**:207.

[16] A bee-keeper in California reported that he found essence of anise very useful in attracting swarms of bees to empty hives, while another bee-keeper in Ohio did not find it of much value. Gleanings in Bee Culture, **40**:482.

[17] This is somewhat similar to the mixture used in "sugaring" for moths. *Psyche*, **19**:195.

[18] The tender stalks are preserved in sugar and sold as a confectionery.

which most strongly sustained his views, while a few particulars were given in regard to his other experiences.[19]

There will be described in the present paper a few of the more interesting experiments performed by Plateau on relatively large and brilliantly colored flowers seldom visited by insects, following which will be given the observations of the writer on similar flowers. Among the familiar species selected by Plateau was a purple-flowered variety of *Clematis Jackmanni* Jack., a hardy perennial vine widely cultivated both in Europe and America. The flowers are nectarless, but bees obtain from them a small amount of pollen. A vine of *C. Jackmanni superba* is described by Plateau as covering a wall three meters in height and displaying many hundred magnificent blue-violet flowers, which are said to have been wholly ignored by insects. On a very warm clear day anisette was introduced into eleven flowers, near each other, and constituting a group by themselves. In the hour following, they were visited by fourteen bumblebees and six flies belonging to the family Syrphidae. In four instances bumblebees examined adjacent flowers which remained in their natural condition.

The facts related by Plateau are not called in question; but it should be noted again that the ungarnished flowers possessed only conspicuousness and pollen, while the eleven flowers containing anisette possessed conspicuousness, pollen, an agreeable odor and a sweet liquid; evidently color was not here brought directly into competition with odor. Let us now endeavor to determine whether the purple flowers are as completely neglected by insects as Plateau supposed; and whether insects can not be induced to visit them in large numbers without the addition of an agreeable odor! The purple-flowered *Clematis* on which my observations were made was a small vine bearing only eleven flowers wholly or partially expanded. The flowers were of large size, pale purple, nectarless, and odorless. As regards brilliancy of coloring and number, they were at a great disadvantage compared with the inflorescence described by Plateau. They were very frequently examined during the entire period of blooming.

[19] Plateau, F., "Recherches expérimentales sur les fleurs entomophiles peu visitées par les insectes rendues attractives au moyen de liquides sucrés odorants," *Mem. de l'Acad. roy. de Belgique*, 2me sér., **2**:1–55, 1910.

On June 11, 1912, a warm clear day, a honey-bee was observed at 12:35 p. m., gathering pollen, also a wild bee which flew away so quickly that it could not be determined. The honey-bee visited four or five flowers before returning to the hive. A few minutes later a second and third honey-bee came for pollen; and during the succeeding hour one or two workers were constantly visiting the flowers for this purpose. One of them remained for a long time, and the loads of purple pollen in the pollen-baskets were plainly visible. Two females of *Halictus craterus* came for pollen. A bumblebee inspected the flowers, but did not alight. A small undetermined bee flew from flower to flower apparently looking for pollen. At 1:35 p. m., there were no insects on the flowers; but a little later a small species of *Halictus*, and also a female of the larger *Halictus craterus* arrived and removed all the pollen remaining available. On three other occasions a female *Halictus craterus* was seen collecting pollen, which in one instance colored purple the under side of the abdomen and the brushes on the posterior legs. No attempt was made to capture any of the bees since this would have lessened the normal number of visits.

The nectarless flowers of *Clematis* were not, therefore, entirely neglected by insects; but were visited by a number of bees sufficiently large to remove all the pollen they produced, and to have effectively pollinated the stigmas had they been in a normally receptive condition, and as this is all that is required, additional visits would have been of no advantage. The sterility of the flowers is not thus due to the absence of pollen-carriers as Plateau supposed. The flowers should be examined immediately after anthesis before the pollen has been removed; since Plateau makes no mention of the pollen he probably did not observe whether it was removed or not.[20] I inspected the flowers many times without finding any insects, and it is easy to understand how a casual observer might gain the impression that they were entirely neglected. Plateau's failure to discover insects on the flowers in their natural condition may have been partly due to an insufficient number of observations, partly to location, and partly to the absence of suitable species of bees. Bumblebees are not well adapted for gathering the scanty supply of pollen, and prob-

[20] Cowles has suggested that Plateau failed to see the earlier visits of his insects, Cowles, H. C., "Insects and Flower Colors," *Bot. Gaz.*, **39**:70, 1905.

ably seldom make the attempt. After the pollen has been entirely removed there is, of course, no reason why bees should continue their visits. In an earlier paper I have shown that flowers frequently visited by bees were almost entirely deserted when the corollas were removed; there is, therefore, good reason to believe that the purple sepals of *Clematis* attract the attention of insects.

I next proceeded to place on a few flowers an odorless sweet liquid for the purpose of ascertaining whether they would not be visited by bees in large numbers. White granulated sugar dissolved in equal parts of water yields an odorless and colorless syrup, as is admitted by Plateau.[21] June 16 and 17 were cloudy, rainy days, but the 18th was fair. At 8 o'clock a. m., a small quantity of syrup of sugar was placed on three flowers. No visitors were observed until 9:15, when two females of *Halictus craterus* began feeding on the syrup; five minutes later there was a honey-bee at the syrup and a female of *Halictus craterus* gathering pollen. Sugar syrup was now placed on a fourth flower. At 10:00 o'clock there were three honey-bees and one female *H. craterus* feeding on the syrup, a second female *H. craterus* on a flower without syrup, and a third hovering in the air. Ten minutes later a honey-bee left a flower on which there was syrup and flew to two empty flowers; but, after carefully examining their centers and finding nothing, it returned to the flower on which it had previously been at work. The bees were compelled to learn by experience which flowers contained syrup and which did not. I replenished the supply of syrup from time to time as it was consumed, and at 12:15 p. m., there were seven honey-bees sucking on the flowers. On the morning of June 19 I again put syrup of sugar on the flowers, and presently three or four bees were at work. It seemed needless to continue the experiment further, for the bees came from my apiary and it was only a question of time and of supplying the syrup in sufficient quantity to have attracted them in great numbers. During the latter part of this experiment there were eighteen flowers in bloom. Plateau's assumption that the flowers would not be visited unless they were given an agreeable odor was shown to be wholly erroneous; the addition of an odorless sweet liquid secured the visits of insects in far greater numbers than were observed by him.

[21] Plateau, F., " Recherches expérimentales," etc., p. 19.

Another common flower selected by Plateau for experiment was the edible garden pea, *Pisum sativum* L. The flowers are rarely pollinated by insects, and self-fertilization is almost invariable. It was for this reason selected by Mendel for his celebrated experiments in hybridization. He says: "Among more than 10,000 plants which were carefully examined there were very few cases where an indubitable false impregnation had occurred." [22] During four summers, however, Müller frequently saw the flowers visited by both sexes of *Megachile pyrina*, and the females both sucked nectar and collected pollen.[23] Plateau's observations were confined to walking on two occasions through many cultivated fields of peas, in one of which he saw a single *Bombus agrorum*.

Plateau introduced anisette into a dozen, or, on one day, two dozen flowers of *Pisum sativum* growing in his garden, which were carefully observed for from one to three hours on five days. The anisette was renewed each day. Twenty visits were made by species of *Bombus* and *Megachile*; and ten visits by flies and small bees which could not possibly effect pollination. Plateau attributed the small number of insects attracted by the odoriferous liquid food to frequent interruptions by rain.

The flowers of the common garden pea are rarely visited by insects, not because they are nearly odorless and the coloration is of no value, but because of the difficulty of depressing the carina. This species no longer exists in the wild state; and, according to De Candolle, was probably introduced into Europe from Western Asia.[24] Müller says: "In its original home the pea no doubt adapted itself to some strong and at the same time diligent and skillful species of bee, which could easily depress the carina, and was plentiful enough in ordinary weather to act as the regular fertilizing agent. Under such conditions, the advantages of firm closure would outweigh the disadvantages. In our climate the pea fails to find bees adapted to its flowers, and it would be much better for it under these altered conditions to have its flowers less firmly shut." [25]

During the summer of 1912, I saw the flowers of the garden

[22] Bateson, W., "Mendel's Principles of Heredity," p. 342. Bateson is of the opinion that Thrips may be a source of error.
[23] Müller, H., "Fertilization of Flowers," p. 214.
[24] De Candolle, A., "Origin of Cultivated Plants," p. 329.
[25] "Fertilization of Flowers," p. 214.

pea visited a few times by females of *Bombus fervidus* only; but in other seasons I have occasionally observed honey-bees endeavoring to find nectar in the flowers. The visits of the bumblebees were made in the legitimate way, but I was unable to approach near enough to determine whether the carina was actually depressed or not. In each instance, the bee visited only three or four flowers, probably because it experienced difficulty in obtaining the nectar which was not abundant.

In this connection, it is a matter of surprise that Plateau passes over the flowers of the sweet pea, *Lathyrus odoratus* L., without mention. This species belongs to the same family as the garden pea, to which it is closely allied in form and structure, though differing in details. Although the blossoms have a strong and pleasant odor suggestive of honey in addition to the most brilliant hues, it is yet more sparingly visited by insects than the garden pea. According to Plateau, the nearly scentless flowers of the garden pea require an agreeable odor to attract insects; but the fragrance of the sweet pea, which is so pleasing that any effort to improve it would be as futile as the proverbial attempt to paint the lily, does not give the inflorescence any permanent advantage over that of the garden pea. If the absence of insects from the garden pea shows that the influence of its coloration is of no significance, then it may be inquired does not the absence of insects from the sweet pea prove that both color and odor are of no importance? Bees neglect to visit the sweet pea frequently not because these two allurements are of no benefit, but because they have learned from experience that they can not obtain nectar. To attract numerous visits, both the garden pea and the sweet pea require an available food supply.

Place a honey-bee on one of the wings of the sweet pea, and it is at once apparent that it is neither large enough nor strong enough to depress the carina. Repeated examinations of the flowers continued through several weeks of the summer of 1912 failed to reveal a single visit by any species of bee. But by September 22, the autumnal honey-flow from the golden-rods was over, and the honey-bees were at liberty to give more attention to the few other flowers still remaining in bloom. On this date I repeatedly saw honey-bees alight and examine the flowers of the sweet pea, but they made no attempt to depress the keel. One probed diligently between a wing petal and the

keel, while another sought for nectar under the calyx lobes, at one time standing on the back of the standard. None of their efforts proved effectual.

Neither can any of our Maine bumblebees depress the carina. On September 26 I saw a female *Bombus fervidus* visit illegitimately twenty flowers in succession. Standing sideways on the flower, clinging to one of the wings and the calyx, she inserted her tongue in a crevice between the standard and a wing petal. Subsequently she robbed many other flowers of their nectar in the same way. The nectar was also obtained in a similar manner by a worker of *Bombus consimilis.**

Until the summer of 1912 I did not suppose that any of our indigenous bees could properly pollinate the flowers; but on August 17 and September 15 and 22, a female leaf-cutting bee, *Megachile latimanus*, was observed to visit the flowers legitimately. She manifested so little fear that I was able to watch her movements at close range. The stigma protruded for a long distance, touching the abdominal scopa on one side and on the other the brush of hairs on the tibia of the posterior leg. Both brushes were thickly covered with pollen. In England, also, according to Punnett, a species of *Megachile* is able to depress the carina.[26] Müller saw only *Anthidium manicatum* sucking on the flowers.

Neither color alone in the garden pea nor color and odor combined in the sweet pea will induce frequent visits, if nothing is to be gained thereby; but, if an odorless sweet syrup is placed on the flowers, bees will resort to them in large numbers. On the morning of August 16 I placed syrup of sugar on a number of sweet pea blossoms. Three times during the afternoon I found a worker of *Bombus consimilis* feeding on the syrup—probably the same bee in each instance. On the 17th I renewed the supply of syrup, and at about 12:30 p. m., a honey-bee discovered it; an hour later there was three honey-bees. Before the close of the afternoon, four honey-bees and two bumblebees were sucking the syrup, or flying about the flowers to which it

**Bombus consimilis* Cr. is doubtless correctly regarded as a synonym of *B. vagans* Sm., but as the local specimens agree exactly with a set of the three forms of *B. consimilis* obtained from the Ac. Nat. Sci. Phil. the name has been permitted to stand in this paper.

[26] Punnett, R. C., "Mendelism," p. 188.

adhered in small drops. It is evident that they must have occasionally inspected the blossoms, or they would not have discovered the colorless and odorless liquid. By frequently replenishing the syrup, an indefinite number of bees might have been attracted. There was sugar syrup on about ten flower clusters. An available and abundant food supply is required, therefore, to secure numerous and continued visits.

Let us now inquire whether similar results can not be obtained in the case of the garden pea, *Pisum sativum*. On a clear and moderately warm morning (July 31, 1913), at 8:00 o'clock, about forty flowers of this species were dipped in sugar syrup, a few, small drops of the thin, colorless and odorless solution adhering to each corolla. The garden was in a secluded location, which had not been planted previously for many years, and was nearly surrounded on two sides by a tall cedar hedge. During the half hour following, a honey-bee inspected the flowers on another row of peas, but failed to find the flowers garnished with sugar syrup. At 8:40 a. m., a white-banded wasp, *Vespa consobrina* Sauss, was also seen examining the flowers on another row of peas, and presently, more fortunate than the bee, it came to the flowers on which there was sugar syrup. For the larger part of the day this wasp, and a little later a second wasp of the same species, worked diligently gathering the sweet liquid. I recorded many of their visits, but it would be tedious to relate them in detail.

At 9:10 a. m., a honey-bee was observed inspecting ungarnished flowers of the garden pea; it alighted on the carina and then sought unsuccessfully to reach the nectar through the side of the flower. Ten minutes later a honey-bee discovered the flowers with syrup, and subsequently it continued to return to them at intervals until 10:20 a. m., when I closed the experiment. It met with many disappointments as it often examined ungarnished flowers. The pea blossoms were also visited by a yellow-banded wasp, *Vespa germanica* Fab. At 4:00 p. m., I found both species of *Vespa* still resorting to the flowers.

On August 2, a hot, clear day, at 12:30 p. m., forty flowers of the garden pea were supplied with sugar syrup, which was almost immediately found by a honey-bee and a *Vespa consobrina*. At 12:45, a second honey-bee and a *Vespa germanica* came to

the flowers. In another part of the garden a female *Megachile melanophaea* (one of the larger leaf-cutting bees), was observed to visit ungarnished flowers in the normal way. At 1:15 o'clock there were two honey-bees, two *Vespa consobrina* and the small pale blue butterfly, *Lycaena pseudargiolus*, sucking syrup from the flowers; and fifteen minutes later one honey-bee, two *V. consobrina* and two *V. germanica*. The visits continued until 2:45 p. m., when I closed the experiment.

The number of visits by bees and wasps received by the flowers of the garden pea garnished with sugar syrup, during the time they were under observation, was much greater than I had expected. Under the conditions I should not have been surprised had there been no visits by Hymenoptera. On the night preceding August 2 there had been much rain, and the following morning was very foggy, so that the leaves of the pea vines at noon were covered with small drops of water, which could not be distinguished from drops of sugar syrup. The bees made many fruitless visits to flowers without syrup and also to flowers on the wrong row. But both bees and wasps soon learned to confine their attention chiefly to the end of the row with garnished flowers.

There were many small Syrphid flies, as well as larger flies, flitting about among the foliage of the pea vines. Although they not infrequently came to the flowers on which there was sugar syrup, but little importance was attached to their visits, as evidently they might be largely the result of chance. One or two smaller bees belonging to the genera *Sphecodes* and *Prosopis* were also among the visitors. But the larger aculeate Hymenoptera, whose visits are manifestly purposive, were regarded as much better adapted for observation than small, little specialized insects. It was conclusively shown that an available food supply, without the addition of an agreeable odor, would induce numerous visits of honey-bees and social wasps to the odorless flowers of *Pisum sativum*.

" The many horticultural varieties, known under the name of *Petunia hybrida* and cultivated in all gardens, have resulted, as is well understood, from crossings between *P. nyctaginiflora* Juss. and *P. violacea* Lindl. They offer this very interesting peculiarity, from the point of view of the present work, of receiving no visits from the domestic bee, notwithstanding the brilliancy and dimensions of their beautiful, infundibuliform, white,

rose, violet, or purple flowers."[27] Plateau, however, observed visits by many bumblebees, and species of Diptera belonging to the genera *Eristalis* and *Syrphus*.

Plateau employed in his first experience a large group of Petunias, surrounded by other plants, as *Tagetes patula* and *Scabiosa atropurpurea*, attractive to bumblebees, flies and butterflies; while among the Petunias there was a single stalk of *Borago officinalis* which alone was visited by honey-bees. On a clear but cool August morning, at 9:30 o'clock, he introduced the odoriferous juice of cooked cherries into six flowers near the stalk of borage. At 3:30 p. m., of the same day, the honey-bees discovered the cherry juice and entirely abandoned the borage flowers for the Petunias. During an hour there were fourteen arrivals, each individual visiting many of the garnished flowers, and rarely a few of the empty flowers. Essentially similar results were obtained in Plateau's other observations on Petunias.

The two common species of *Petunia* endemic to South America have long narrow tubes, are strongly scented in the evening, and are either adapted to crepuscular Lepidoptera or are ornithophilous; in either case we should not expect to find honey-bees among their legitimate pollinators. The hybrid forms of cultivation, moreover, are destitute of nectar; and even if it were present the throat of the corolla is so obstructed by the filaments and style that it would be inaccessible to them. Plateau asserted that an odoriferous syrup was required to attract visits by honey-bees, but it can readily be shown that the presence of an odorless, sweet liquid will render their visits very numerous. A medium sized group of single-flowered Petunias of various colors was selected for my observations.

On July 31, 1913, there were only two flowers in bloom, into both of which I introduced sugar syrup. A bumblebee inspected both flowers but overlooked the syrup. On the 2nd there were two fully expanded flowers, and one which had wilted and closed. A honey-bee examined all three, and remained a long time in one of the open flowers. As the sugar syrup had evaporated, the supply was renewed. The honey-bee returned and thirty minutes later was still visiting the flowers. On the following day a female *Bombus consimilis* was a visitor.

[27] Plateau, F., "Recherches expérimentales, etc." *Mem. de l'Acad. roy. de Belgique*, 2me sér., **2**:46, 1910.

On August 10, I introduced sugar syrup into nearly all the expanded flowers. *Vespa consobrina* was a constant visitor throughout the day, and subsequently *Vespa germanica* was also observed on the inflorescence.[28] At 2:30 p. m., a honey-bee appeared and continued its visits for half an hour. The day following was very cold and windy for mid-summer; but the 12th was clear and warm. At 9:05 a. m., I introduced sugar syrup into the expanded flowers. A honey-bee was soon at work, and by 11:00 o'clock the number had increased to three; at 12:45, there were four honey-bees and a *V. consobrina*; at 2:35 there were five honey-bees and a *V. consobrina*; and at 6:00 p. m., the wasp and six honey-bees. The number of flowers in bloom was about thirty-five. The weather continued fair on the 13th, and in the morning I found four honey-bees on the flowers. A new supply of sugar syrup was provided, and by 9:10 a. m., there were twelve honey-bees at work. Manifestly, it was needless to continue the experiment further. Thus, without the addition of an agreeable odor, but merely by introducing a supply of an odorless, colorless syrup the visits of honey-bees were induced in great numbers.

Although sugar syrup was not again introduced into the flowers, on August 14, 15 and 16 I saw honey-bees examining the inflorescence, doubtless remembering their former experience. On September 2, a honey-bee alighted on two flowers and examined others; by this time most, if not all, of the flowers into which syrup had been introduced had wilted. Bumblebees were also seen to visit the flowers occasionally, but not finding nectar, they did not remain long. There were many small Diptera flying about the foliage of the Petunias, but little or no significance was attached to their visits. A small bee of the genus *Halictus* also alighted on the corollas.

Pelargonium zonale Willd., says Plateau, is one of the more noteworthy forms of plants with very brilliant flowers, which are almost wholly ignored by insects; the beds of scarlet Pelargoniums, commonly called red geraniums, of which there are a profusion in public gardens, permit us to establish this fact each year. A large bed of *Pelargonium zonale* displayed more than fifty umbels of scarlet flowers; into three umbels on the left side

---

[28] For the determination of the specific names of these wasps I am indebted to Mr. S. A. Rohwer.

of the bed Plateau introduced the cooked juice of cherries, and in two umbels on the right side anisette was used. Immediately many flies belonging to the families Muscidae and Sarcophagidae, and later two Syrphidae and three wasps were attracted to the odoriferous liquids. The clusters which remained in their natural state are said not to have received a single visit.

A large plant of *Pelargonium zonale*, of the variety called "General Grant," produced in my garden during the larger part of the summer of 1912 numerous bright scarlet umbels. The nectaries had disappeared and the stamens were largely petaloid so that the flowers yielded neither nectar nor pollen; notwithstanding frequent inspections no insect visits were observed during the larger part of the season. On September 23, at 1:00 p. m., odorless sugar syrup was introduced into two umbels near the center of the plant. From the 23rd to the 26th, no insects found the syrup, which was renewed from time to time as it evaporated. The 26th was warm and clear, and in the afternoon I saw a honey-bee inspect a cluster of flowers near the ground, but it did not alight. The weather continued fair on the 27th, and at 7:00 a. m., there were no insects on the flowers; but at 9:00 o'clock there were, at least, a dozen honey-bees feeding on the syrup, which was speedily consumed. There were six other fully expanded umbels on which there was no syrup, and it was interesting to note how the bees searched them again and again in their efforts to find more of the edible liquid. Two other umbels with a few buds partially open were also carefully examined. Their attention at first was entirely confined to the gaudy flowers, but later they discovered some of the liquid, which had dripped on a few leaves, and removed it. Their number continued to increase so long as I supplied the syrup. Later they flew to a bed of *Portulaca grandiflora* Lindl., to the inflorescence of which they had never before been seen to pay any attention, and inspected flower after flower but seldom alighted.[29]

Evidently the bees had learned from past experience to associate the presence of nectar with conspicuousness, and though they had never found any food in these particular flowers, they had no doubt continued to occasionally inspect them, as in the

[29] During a part of the time this experiment was in progress one of the colonies in my apiary was allowed to remove the honey from a few partially filled combs; and it subsequently occurred to me that this probably stimulated the bees to search the flowers more diligently for nectar.

single instance observed on the 26th, when a bee inspected an empty umbel but failed to visit those containing syrup. After they had found syrup on two of the umbels, they examined all the others very thoroughly, and also other flowers in the garden previously neglected. They discovered the syrup on the flowers long before they did that which had dripped on a few leaves, and the discovery of the latter was incidental to their visits to the flowers. The bright coloration was clearly an advantage in this instance in enabling honey-bees in large numbers to find the odorless sweet syrup. Obviously highly specialized bees are much better adapted for the purpose of such an experiment than the common flesh-flies observed by Plateau.

Plateau made many additional experiments in the course of which he introduced odoriferous syrups into the flowers of *Lilium candidum* L., *Passiflora adenophylla* Masters, *Œnothera speciosa* Nuttal, *Linum perenne* L., and *Convolvulus sepium* L., with the result that insects in variety were attracted. But it is unnecessary to consider his experiences further since insects in large numbers may also be attracted to conspicuous, neglected flowers by means of an odorless sweet liquid. Since Plateau knew that sugar syrup was odorless it is natural to inquire why he failed to employ it in control experiments. On four occasions he did introduce syrup of sugar into the flowers of *Lilium candidum*, in three instances into two flowers and in one instance into six flowers. He says that, as he foresaw, syrup of sugar without odor did not show any power of attraction.[10] But a small number of Diptera, as *Syritta pipiens*, *Melanophora roralis*, *Anthomyia radicum* and *Calliphora erythrocephala*, did find the syrup and profit by their discovery. No information is given as to the length of time the flowers were under observation. The number of visits received, however, was about the same as in the case of *Polygonum Convolvulus*, when anisette was added to eight groups of flowers on a very warm clear day. Certainly the list of Diptera recorded gave promise that many visits would have been received had the supply of syrup been continued for a longer period. *Lilium candidum* is a campanulate flower two or three inches long adapted to pollination by hawk-moths, and it is easy to understand that some time might elapse before the deeply concealed syrup was found by Hymenoptera. No

[10] "Recherches expérimentales sur les fleurs entomophiles," etc., p. 19.

mention is made of the use of sugar syrup in any other control experiments, an omission which can hardly be regarded as excusable.

It seems desirable, therefore, in this connection to give a few additional instances observed by myself, where the introduction of sugar syrup resulted in frequent visits of bees. A group of *Zinnia elegans* Jacq., in my garden, was almost wholly neglected by insects. On the morning of August 16, I introduced syrup of sugar into several capitula, renewing the supply the following day. During the forenoon of the 17th, a honey-bee examined the ray flowers of two ungarnished capitula, and then, coming to a head, containing syrup, sucked for a short time. Later a worker of *Bombus consimilis* found the syrup. At 12:30 p. m., there were on the flowers two honey-bees and two worker bumblebees, *Bombus consimilis* and *B. terricola*. At 3:30 p. m., there were seven honey-bees and one bumblebee on the flowers—there was syrup in a dozen capitula. The honey-bees also examined the capitula which remained in their natural condition. The experiment was now discontinued. Three days later, on August 20, a honey-bee, undoubtedly one of the former visitors, examined many capitula; evidently it remembered its previous experience.

The brilliantly colored flowers of the scarlet runner, *Phaseolus multiflorus* Willd. var. *coccineus* Lam., contain nectar; but owing to the difficulty of depressing the carina, are much neglected by insects. Occasionally in this locality females of *Bombus fervidus* visit the flowers legitimately. I have also seen a honey-bee for several hours fly from flower to flower inserting its tongue in the opening beneath the standard, and apparently able to reach a very small quantity of the nectar. On the morning of August 16, I put sugar syrup on a few corollas, and during the afternoon there were always from four to six bees on the flowers. They also inspected flowers on which there was no syrup. On the 17th, I renewed the supply of syrup and the bees continued their visits during the entire day.

Honey-bees have not sufficient strength to depress the carina and obtain the nectar normally; but if the nectaries are punctured they will then visit the flowers in great numbers. Every year the scarlet runner is under cultivation in my garden, but I have never known bumblebees to bite holes in the flowers except

in 1908. On August 14 of that year, the vines were in full bloom, and there were present many workers of *Bombus terricola*, which perforated the flowers as fast as they matured—so far as I could discover not a single blossom escaped. The holes were all on the under side of the calyx on the left hand side, which may be explained by the fact (also observed by Müller[31]) that the more powerful bees almost invariably alight on the left ala. The honey-bees promptly discovered the holes and used them most diligently for extracting the nectar. There was no pretence on the part of either honey-bees or bumblebees of making normal visits. The absence of bees from the flowers of the scarlet runner does not, therefore, prove that their brilliant hue is of no advantage, or that an agreeable odor is required, for it is only necessary to render the nectar easily accessible by punctures to induce the visits of bumblebees and honey-bees in great numbers.

The correlation existing between the accessibility of nectar and the number of honey-bees present is also most instructively shown by the inflorescence of red clover, *Trifolium pratense* L. The flowers are pollinated chiefly by bumblebees, which are frequent visitors, and in their absence are largely sterile. An historical illustration is the well-known experience of the agriculturists of New Zealand, in which country at the time of its discovery there were neither honey-bees nor bumblebees. In consequence the yield of seed did not become commercially profitable until in 1855, when about one hundred bumblebees were imported from Europe.[32]

The nectar of red clover is secreted at the base of a tube a little over 9 mm. in length, where it is beyond the reach of the tongue of the honey-bee. This has occasioned much regret among bee-keepers, for the flowers not only secrete nectar very freely but the quantity is not greatly affected by weather conditions. Repeated attempts have been made to develop a strain of red clover bees, but the gain in tongue length has invariably

[31] Müller, H., "Fertilization of Flowers," p. 216. Both honey-bees and bumblebees almost invariably alight on the left ala. The reason for this is that the spirally coiled carina closes the entrance beneath the standard on the right hand side. Usually the alae stand apart, but when one occasionally overlaps the other, honey-bees alight on the center. Bumblebees visit the flowers of the common, garden bush beans in a similar manner.

[32] Knuth, P., "Handbook of Flower Pollination," translated by J. R. Ainsworth Davis, 2:292. Jarvis, P. D., "Bumblebees that Fertilize Red Clover," *Rep. Ent. Soc. Ont.*, **36**:128. Graenicher, S., "New Zealand's Experience with the Red Clover and Bumblebees," *Bull. Wis. Nat. Hist. Soc.*, **8**:166.

proved only temporary. Under normal conditions, then, honey-bees do not frequently resort to the red clover fields; but occasionally in very dry weather the floral tubes become so short that large yields of honey are obtained. Two or three times during the last thirty years at Borodino, N. Y., red clover has been a very valuable source of honey; and one season fully sixty pounds, on an average, to a colony was secured.[33] An apiarist in Michigan reports that in one year his bees stored 500 pounds of pure red clover honey as surplus.[34] The black bees stored none, the hybrids only a little, while the bulk of the 500 pounds was gathered by Italian bees. The length of the tongue of the common black bee is 6 mm., of the pure Italians, not over 7 mm., while that of the hybrids is intermediate. Thus there was presented the singular spectacle of fields of red clover visited by thousands of Italian bees, while the black bees were absent. Had the drought shortened the corolla tubes another millimeter the nectar would have been accessible to black bees, and they, too, would have been present.

But undoubtedly the most remarkable illustration ever recorded of the relation of rainfall to the length of the corolla-tubes, and consequently of the accessibility of the nectar to honey-bees, was observed by an apiarist at Medina, Ohio. Of two apiaries belonging to him one is located near Medina, and the other two miles north of that city. A few years ago (1906) there was a drouth at the north bee-yard, and the floral tubes of the red clover were so much shorter than usual that honey-bees were able to reach the nectar. When one of the farmers began to cut his field of red clover that season, the cutter knives of the mower stirred up so many bees that they attacked the horses and their driver. So numerous and pugnacious were they that it looked as though they would prevent anyone from cutting off their supply of honey.

Singularly enough at Medina and the south bee-yard, there was an abundance of rain. Here, when he went over a big field covered with a luxuriant growth of red clover scarcely a bee could be found. The corolla-tubes were so long that the bees could not obtain the nectar, and consequently, there were none on the clover heads. Thus two bee-keepers, living only a few

[33] Doolittle, G. M., " Honey from Red Clover," *Gleanings in Bee Culture,* **34**:993.
[34] Hutchinson, W. Z., " Red Clover," *The Bee-Keepers' Review,* **21**:342.

miles apart, might have arrived at diametrically opposite conclusions as to the value of red clover as a honey plant.[35]

It is clear that the presence or absence of honey-bees in large numbers on the flowers of red clover is not determined by the color or odor, but by the accessibility or inaccessibility of the nectar. Drouth may not render the nectar accessible more than once in ten years, but when it does happen, the bees promptly avail themselves of the opportunity. Evidently they must inspect the flowers each season, but, finding no booty, they do not often repeat their visits. The utter inconsistency with the facts of the claim that the absence of insects from certain conspicuous flowers proves that bright coloration is of no advantage and that an agreeable odor is a necessity, could not be better shown than in the instance where the Italian bees were able to obtain the nectar and the black bees were not.

The flowers of alfalfa, *Medicago sativa* L., a leguminous plant very extensively cultivated in the west for forage, offers very similar phenomena. In the irrigated regions of California and Colorado, nectar is yielded so abundantly that alfalfa surpasses all the other local honey plants in importance, even the famous purple, black and white sages of the former state. But in Kansas, for example, the results are strikingly different. In the Western part of the state along the river bottoms the flowers can usually be depended on for nectar during most of the season, while around Topeka, bees only occasionally visit the bloom. A bee-keeper who has lived in Eastern Kansas for thirty-five years states he has never seen a bee on the flowers, or known of a pound of alfalfa honey being produced in that section.[36] Where alfalfa, then, secretes nectar freely the vast acreage is constantly the resort of millions of bees; but in localities where it is nectarless,

---

[35] Root, E. R., "Red Clover as a Honey Plant," *Gleanings in Bee Culture*, **34**: 990. The three apiarists cited in this article are careful observers and recognized authorities on bee-culture. Buttel-Reepen has remarked: "It seems to me that the biological knowledge concerning *Apis mellifica* which has been gained by practical bee-keeping has scarcely entered scientific literature . . . In proof of this there are the vague, defective assertions which are found in the newest editions of scientific works." "Are Bees Reflex Machines," p. 1.

[36] Root, E. R., "Bee-keeping in the Semi-arid Regions of Oklahoma, Kansas and Nebraska," **41**:345. In the eastern states of North America, white clover, *Trifolium repens* L., is the foremost honey plant, and the domestic bee stores from its bloom annually hundreds of tons of an excellent, white honey; but in France and Switzerland it yields no appreciable quantity of nectar and one may travel several kilometers and not see a bee on it. "White Clover in Europe," *Am. Bee Journal*, **53**:331.

their visits are so rare that the flowers appear to be entirely deserted through a long series of years. Honey-bees do not usually visit the flowers legitimately, but procure the nectar through a crevice in the side.

An excellent illustration on a scale of great magnitude showing that honey-bees are guided by the memory of past experience in gathering nectar is furnished by the honey-flow of buckwheat, *Fagopyrum esculentum* Moench., which Buttel-Reepen describes as follows:

"If colonies stand in buckwheat, the flight is lively in the mornings until ten o'clock; then it lessens, and is entirely quiet for the greater part of the day, beginning vigorously again the next morning. The buckwheat nectar flows only in early morning; so, as the nectaries dry up, the bees fly out a couple of times and then discontinue their vain flight. In spite of the shimmering sea of flowers, *in spite of the strong fragrance*, only a few bees may usually be found after ten o'clock in the buckwheat field." [37]

The period of time during which the flowers of buckwheat secrete nectar varies in different localities. In this region the bees continue to work on them, according to observations made by a young friend of the writer, until about 12:30 p. m. Their visits then quickly decrease in number until about 1:00 o'clock, when they cease entirely. But for an hour or more afterwards, the bees may be seen occasionally flying from blossom to blossom, pausing, however, for only an instant, as they apparently discover at once that the flowers are now nectarless. At Delanson, N. Y., buckwheat yields nectar most abundantly between 9:00 o'clock in the morning and 2:00 p. m. A bee is seldom at work on it much earlier or much later, notwithstanding there are hundreds of colonies of bees in the vicinity. In parts of the west, buckwheat is a more uncertain honey plant than in the east and in some years the flowers fail to become nectariferous, when they are almost wholly deserted by bees.[38] Again a sudden shower followed by a fall in temperature may bring the buckwheat harvest to an abrupt and premature close in August, when ordinarily it would continue into September. Such an interruption of the

[37] Buttel-Reepen, H. V., "Are Bees Reflex Machines?" translated by Mary H. Geisler, p. 29.
[38] Root, A. I. and E. R., "The A B C and X Y Z of Bee Culture," p. 71.

honey season occurred at Delanson in 1906. For several days a hive on scales had shown a gain of eight pounds a day; but during the night of August 24 there was a light shower and a decline in temperature of 11 degrees F., after which the hive on scales did not show a gain of half a pound any day that fall. The bees immediately ceased visiting the flowers, and in countless thousands attempted to rob each other and the honey house.[39] Owing to the intermittent nature of the flow of nectar, bees are more irritable during the buckwheat harvest than during that of any other plant. The time of the flight of the bees thus always coincides with the period of active secretion of nectar, or if the flowers are nectarless they neglect them almost entirely.

The preceding experiments and studies of honey plants show that honey-bees learn from observation and are guided by the memory of past experience. Flowers rich in accessible food supplies receive numerous visits, but if for any reason the flow of nectar suddenly ceases the bees immediately discontinue their visits. If the inflorescence of a plant species yields abundant nectar in one locality but is devoid of nectar in another, even though only a few miles intervene, the flowers in the former place will be frequently visited and in the latter deserted. But honey-bees do occasionally visit and examine conspicuous flowers from which they can not obtain food materials, and it is upon this premise that the argument of the present paper is based. *A priori* reasoning alone would lead the floroecologist, who believes that conspicuousness is an advantage to flowers to this conclusion, thus Campbell remarks that "it is safe to say that no showy flower is entirely destitute of insect visitors."[40] Much evidence has already been adduced in support of this statement, but it is desirable to give additional observations, made especially for this purpose. The casual observer will often fail to discover a single visitor, and may easily conclude that they never attract the attention of insects; but long continued investigation proves this to be a mistake.

The variegated flowers of the Sweet William, or bunch pink, (*Dianthus barbatus* L.), display the most vivid shades of crimson and scarlet; and, as the name indicates, exhale a pleasant fra-

---

[39] Alexander, E. W., "Buckwheat as a Honey Producer," *Gleanings in Bee Culture*, 35:394.

[40] Campbell, D. H., "Plant Life and Evolution," p. 227.

grance. They are adapted to pollination by butterflies and day-flying moths. The nectar, while not abundant, is sufficient in quantity to yield a sweet taste to the tip of the tongue; and it lies at the bottom of a calycine tube 15 mm. long, far beyond the reach of honey-bees. Previous to July 11, 1912, I failed to record a single bee visitor. On this date I saw a honey-bee inspect several clusters of flowers, but it never actually alighted, although flying close to the inflorescence. On the 23rd, a honey-bee visited a few flowers. At about 11:00 a. m., August 6, a warm clear day, two and at one time three honey-bees were observed on the flowers. They were carefully watched for ten minutes, and one of them vainly endeavored, standing in various positions, to reach the nectar by thrusting its tongue down the center of the flower. Others probed between the petals, even looking under the corolla. An hour later, a bee was still found on the clusters; at intervals, wasps and flies also examined the flowers. Observations extending through the entire season show that the flowers are very far from being wholly neglected by Hymenoptera and Diptera, although a few inspections might readily lead to this belief.

The flowers of the bee larkspur (*Delphinium elatum* L.), which are normally pollinated by bumblebees, have so long a spur that the nectar is wholly inaccessible to honey-bees. In my garden they are very rarely visited by insects of any kind. On the morning of July 11, a honey-bee after visiting one or two flowers, desisted from its useless efforts. On July 24, in the afternoon, a honey-bee visited several flowers in an unsuccessful attempt to find nectar. It pushed its tongue as far as possible into the mouth of the spur, and also looked for nectar under the upper perianth segment. On August 4, a bee inspected two blue floral leaves, which had fallen from a flower to the green foliage, thus showing that a single detached petal could gain its attention.

On July 16, a large moth poised before several flowers and obtained the nectar without difficulty; in the evening the white center contrasts so strongly with the blue ground color that the attention of crepuscular Lepidoptera might easily be gained.

During the summer of 1910, no insects were seen to visit the flowers of the pansy (*Viola tricolor* L.). By October 1, nearly all the wild and cultivated flowers had perished, but a few

pansies still remained in bloom. October 7 was cold and rainy, but the day following was clear, warm and calm, and at 10 a. m., a honey-bee spent more than ten minutes on the pansy flowers searching for nectar. Two Syrphid flies (*Eristalis tenax*) were also flying from flower to flower looking for pollen, but making no attempt to find nectar. On the afternoon of the 10th, a worker of *Bombus consimilis* and a male of *B. fervidus* were examining the flowers for nectar; and on the 11th a worker of *B. consimilis* and a white butterfly. Thus the pansies are not so much neglected as at first appeared probable, but in the absence of more desirable flowers are frequently visited by insects.

On the morning of October 28, 1912, two honey-bees were examining the larger, neutral flowers of *Hydrangea paniculata* Sieb., but they soon learned that they were nectarless and passed over to the smaller, perfect flowers. On July 16, a species of *Megachile* visited two flowers of the climbing honeysuckle (*Lonicera Periclymenum* L.), a hawk-moth flower; but its stay was very brief, as it could not reach the nectar. It then flew to another moth flower (*Œnothera biennis* L.), which was closed. Finding no opportunity to get flower food it returned to the honeysuckle; but meeting with no better success than on its previous visit, it abandoned that part of the garden altogether. In the evening, while the hawk-moths were industriously at work on the honeysuckle flowers, they repeatedly inspected large, red roses blooming on a bush a few feet away. The roses are pollen flowers and devoid of nectar, but the hawk-moths were compelled to learn this fact by direct examination. Another pollen flower is the poppy, but before the anthers dehisc honey-bees may often be seen searching for nectar at the base of the petals. Honey-bees have likewise been observed looking for nectar under the calyx segments of flowers belonging to the Labiatae.

Further examples that honey-bees occasionally examine carefully flowers, which are commonly neglected, might be multiplied indefinitely; but sufficient instances have been given for the purpose of the present paper. It has been shown that such visits are actually made, and that they are infrequent because the bees remember their inability to obtain flower food. Nevertheless, in the aggregate they do waste much time in fruitless visits to a great variety of flowers, which for one reason or another

yield no booty; but this loss is reduced to a minimum by their ability to learn from experience. They are able to store up in their brains, as described by Forel, various sense impressions of color, form and spatial position, by which their movements are subsequently guided and which prevent them from indefinitely making useless visits. "It results, therefore, from the unanimous observations of all the connoisseurs that sensation and perception, and association, inference, memory and habit follow in the social insects the same fundamental laws as in the vertebrates and ourselves."[41] But he adds that "the above mentioned faculties are manifested in an extremely feeble form beyond the confines of the instinct-automatism stereotyped in the species."[42]

In closing this paper it is desirable to remind the reader that the visits of bees to flowers are, of course, often influenced by other factors besides the characters of the flowers, as temperature, rainy or foggy weather, the number of insects in the locality, and especially by the blooming period of common plants very rich in nectar. During the honey-flow from the more important honey plants, bees restrict their visits very closely to a single species, and there is no occasion nor would it be for their advantage to pay attention to flowers containing little or no nectar. Plateau himself noticed that when the apricots expanded their flowers, the Hymenoptera abandoned the violets, and he was forced to discontinue his experiments with artificial flowers.[43] During a honey-flow the entire force of field bees of each colony is largely governed by a common impulse, and their attention may be fairly termed obsessional. The hives may then be opened and the honey exposed with scarcely any danger of robbing. Buttel-Reepen tells of a bee-keeper who placed a dish of honey over his strongest colony during the buckwheat honey-flow, and after eight days of good forage the bees had not touched the honey, although it was pure.[44] Manifestly, under these conditions

[41] Honey-bees will not visit bright-hued pieces of paper or cloth, whether large or small, attached to a line and suspended over a bed of flowers, or crude floral groups painted on large screens or walls, because they are not deceived by these objects, or images, any more than ourselves. Cf. Plateau, F., "Le Macroglosse," *Mem. Soc. ent. de Belgique*, **12**:141–80, 1906.

[42] Forel, August, "Ants and Some Other Insects," translated by William Morton Wheeler, p. 21.

[43] Plateau, F., "Les fleurs artificielles et les insectes," *Mem. de. l'Acad. roy. de Belgique*, **1**:24, 1906.

[44] Buttel-Reepen, H. V., "Are Bees Reflex Machines," p. 27.

small groups of conspicuous, nectarless flowers, and even those containing nectar, will be likely to be passed over unheeded.

CONCLUSIONS

Entomophilous flowers are usually characterized by the possession of either bright coloration, or odor, or both, although apparently to some extent the two qualities are mutually exclusive. Both allurements are useful in attracting the attention of insects; but the absence of either conspicuousness, or odor, or both, will not necessarily cause a flower to be neglected if it contains an ample supply of pollen or nectar. But under similar conditions, small, green, odorless flowers, even if rich in nectar, will not be discovered as quickly as nectariferous flowers, which are conspicuous or agreeably scented.[45] On the other hand, the possession of both color and odor will not ensure frequent visits in the absence of available food materials. The experiments afford no evidence that bees visit flowers for the purpose of experiencing an aesthetic pleasure.

Insects, especially bees, occasionally examine the neglected, conspicuous flowers of cultivation; but, obtaining no food materials, or very little, they do not often repeat their visits. Many neglected flowers are pleasantly scented, and the addition of another agreeable odor is neither necessary nor beneficial.

When odoriferous fruit syrups are introduced into conspicuous flowers, commonly neglected, a group of miscellaneous insects, especially Diptera, will be attracted; but the inference that, therefore, color is no advantage and that an agreeable odor is required is fallacious. For the introduction of an odorless syrup into similar flowers will induce insect visits in large numbers; also when flowers, with the nectar inaccessible to honeybees and, consequently, seldom visited by them, have the nectaries artificially punctured, or the floral tubes shortened by drouth, they are then visited by bees in countless thousands without the addition of either an agreeable odor or a sweet liquid. Flowers which in one locality freely secrete nectar and are visited by numerous insects are sometimes in other localities nectarless and almost entirely neglected. Insects, therefore, perceive the colors and forms of neglected flowers, and the rarity of their

[45] Lovell, John H., "The Pollination of Green Flowers," *Amer. Nat.*, **46**:83–107, 1912.

visits is the result of their memory of the absence of food materials, not because the flowers lack an agreeable odor, which is often not the fact.

The flowers into which Plateau introduced odoriferous sweet liquids were thus artificially converted into distinct physiological varieties. Since flowers possessing conspicuousness, an agreeable odor, and a liquid food were opposed to flowers possessing only conspicuousness, it is clear that color was never directly brought into competition with odor—the latter was invariably given the advantage.

Colors and odors attract the attention of insects, but bees in their visits to flowers, previously examined by them, are guided largely by the memory of past experience; they are able to associate different sense impressions and unconsciously make analogous inferences.

THE HARVARD LABORATORY OF ANIMAL PSYCHOLOGY AND THE FRANKLIN FIELD STATION

ROBERT M. YERKES

With two figures

It is now fifteen years since the Director of the Harvard Psychological Laboratory, Professor Hugo Münsterberg, made a place for experimental work on the psychology of infra-human organisms in his laboratory. In 1899, two rooms in Dane Hall were assigned to students of animal psychology, and under the direction of the writer, three investigations were conducted. To meet the needs of an increasing number of workers, an additional room was made available in 1902.

In December, 1905, the laboratory equipment, together with all experimental work in psychology, was transferred to a newly and specially planned and constructed laboratory in Emerson Hall. Here, five rooms, in addition to the Instructor's office and a large amount of space in an unfinished attic, were available for work with animals. The following account of the facilities afforded for this work is quoted from a description of the Harvard Psychological Laboratory, published in 1906:[1]

" Several rooms are fitted up with special reference to the investigation of the various forms of organic movement, animal behavior and intelligence. As one result of several investigations in animal psychology already pursued here, the laboratory has a considerable number of devices for testing and making statistical studies of the senses and intelligence, methods of learning and emotional reactions of animals.

"Adequate provision is made for the keeping of animals in a large, well-lighted, and well-ventilated corner room. Instead of having aquaria built into the room, an aquarium-table eighteen feet long has been constructed to support movable aquaria of various sizes. Whenever it is desirable for the purposes of an investigation, any of these aquaria may be moved to the research-

[1] The Harvard Psychol. Studies, vol. 2, p. 35.

room of the investigator or to such quarters as the special conditions of the experiment demand.

"The vivarium-room contains, in addition to provisions for water-inhabiting animals, cages of a variety of forms and sizes. The largest of these cages, six and a half feet high, six feet wide, and four feet deep, may be used for birds, monkeys, or any of the medium-sized mammals. Cages for rabbits, guinea-pigs, and other small animals are arranged in frames which support four double compartments. Similarly, small cages suitable for mice, rats, and other small rodents are in supporting frames which carry four of the double cages, each of which is removable and may be carried to the experimenting-room at the convenience of the experimenter.

"In a large unheated room above the main laboratory are tanks for amphibians and reptiles. These tanks, since they can be kept at a low temperature during the winter, are very convenient and useful for frogs, tortoises, and similar hibernating animals."

Work progressed satisfactorily in these quarters until the spring of 1913, when the introduction of experimental work in Educational Psychology, rendered desirable a redistribution of space. During the summer of 1913, the unfinished fourth floor of Emerson Hall previously referred to was developed, in accordance with plans prepared by the writer, as a laboratory of animal psychology. The floor plan of this new laboratory is presented in the accompanying figure 1.

Ten rooms, in addition to an office for the director of the work, are now at the service of students of animal psychology. Of these rooms, several were especially planned and have been at least partially equipped for definite lines of inquiry. Thus rooms 40 and 41 have been built about the Yerkes and Watson apparatus for the study of the several aspects of vision in animals. Preliminary studies of vision by simpler rough and ready methods are conducted in other rooms of the laboratory, or at the Field Station described below, and the more elaborate apparatus is used only for accurate and thorough-going investigations. By means of our varied visual equipment, it is possible to study color, intensity, size, form, and distance perception with a degree of exactitude which heretofore has been exceptional in connection with studies of animal behavior.

Room 42 is equipped with the Watson circular maze and the

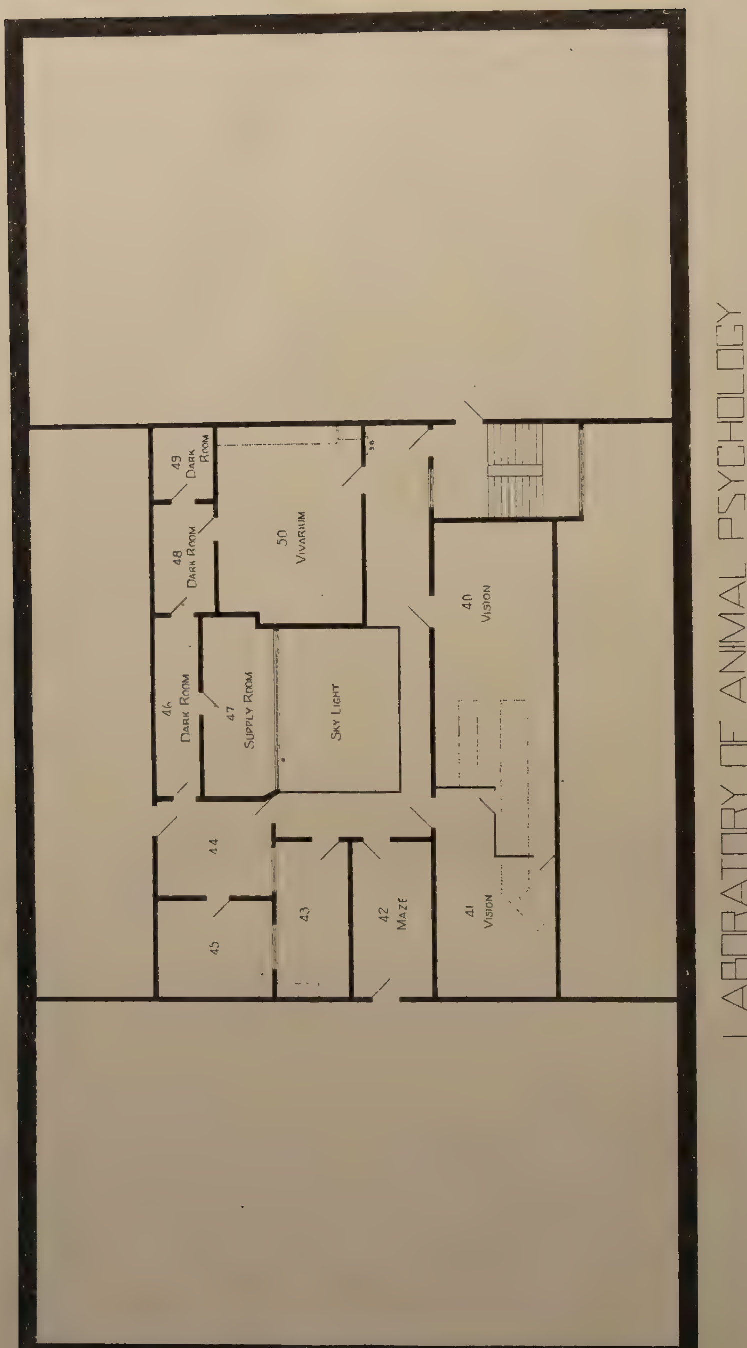

FIGURE 1. Floor plan of the new Harvard laboratory for the study of animal psychology.

Yerkes and Kellogg graphic record device. The latter enables an observer to obtain accurate records of distance and errors, in addition to those of time, in all maze experiments. Thus, the value of the maze-method is trebled. This improved apparatus demands stability, and, although it may readily enough be moved from room to room, it is eminently desirable to have a suitable place reserved for it, so long as the maze method maintains its present importance and promise as a comparative method and offers so many obvious possibilities of improvement.

The rooms numbered 43, 44 and 45 are daylight rooms as is also 42, which may be employed as occasion demands. At present, two of them are used for studies of problems of heredity in rats and mice. Later, the Hamilton insoluble problem multiple choice apparatus and the Yerkes soluble problem multiple choice apparatus will be installed in this group of rooms. These devices demand a special recorder-room. It is our purpose to install the recorder for both outfits in one room while placing the respective reaction devices in separate rooms. These two sets of multiple choice apparatus will render possible in this laboratory or at the Field Station (since we propose so to construct the apparatus that it shall be readily movable) the study of ideational reactions, in a variety of animal types, in such wise as to furnish directly comparable data of reaction.

The line of dark-rooms numbered 46, 48 and 49, is especially convenient because it may be used either in sections or as a whole. A supply of compressed air is delivered to room 49, and it is intended that in this room, in conjunction with room 48, there shall be installed apparatus demanding air under constant pressure for varied studies of olfaction and audition.

A store room, number 47, provides adequate space for supplies in the shape of food stuffs, bedding or litter, small cages, and packing or transportation boxes. Storage space for larger apparatus and materials is afforded by a room to which entrance is given by the doorway indicated in room 42.

Finally, room 50 is the "animal living room" of the laboratory. The floor of this room is water proof so that cages and aquaria may be thoroughly washed and the floor flushed at need. In this vivarium are set cages for a variety of vertebrates. At present, the laboratory is supplied with cages especially designed for mice, rats, guinea pigs, rabbits, cats, monkeys and birds.

A large aquarium table, upon which any desired form of aquarium may be placed, provides for the housing of amphibians and fishes.

The writer's students' training course in animal psychology is conducted in a class-room and lecture room on the third floor of Emerson Hall. The space of the laboratory on the fourth floor is, therefore, wholly available for research.

The rooms of the new laboratory are supplied with water, gas, compressed air, and a variety of electric currents. The latter are conveniently delivered from boards located in each room. In every room there are available 110 volt direct and alternating currents, as well as currents from Edison storage batteries which are located in the battery room of the main laboratory. A conveniently placed and well constructed switch board (S. B. of Figure 1) in the corridor of the laboratory, provides for the distribution of these storage currents. This board is fitted with miniature Weston switch board voltmeter and ammeter, and with taper plugs.

Realizing the extreme need for apparatus in animal investigations which shall, in a large measure, eliminate the experimenter from the situation to which the animal is expected to respond, the writer, in planning this new laboratory, has attempted so to arrange spaces that automatic setting, actuating and recording devices may readily be placed in rooms adjoining those in which the animal is responding. Heretofore, the majority of students of animal behavior have deemed themselves competent and able to observe and record accurately the doings of their subjects. That this, however, is not the case is clearly proved by numerous instances of misobservation and misinterpretation of reactions. We have, for example, twice discovered in this laboratory that dogs which were presumably responding to a definitely arranged experimental situation were actually responding to certain unconscious movements of the experimenter. The only safe and sure way to avoid such risks is to provide mechanical recorders which shall at least enable the experimenter to separate himself widely from his reacting subject.

We have striven for flexibility and adaptability in this new laboratory of animal psychology while arranging for the development, in designated spaces, of specific forms of apparatus. So far as the conduct of experimental work under highly con-

trollable and reasonably controlled conditions is in question, the laboratory, with its instrumental equipment, is excellent. But in addition to the ever present need of the development of new methods and the opportunity for the advantageous installation of new apparatus, the writer has felt as a still more urgent and important need, the supplementation of the laboratory by facilities for field work.

It would appear to be self-evident, yet the attitude of many experimental students of animal behavior seems to contradict the statement, that every student of animal life should be familiar with the objects of his interest in nature as well as in the laboratory; that he should possess, as a basis for evaluating the results of experiments, intimate knowledge of the instincts, habits, temperaments, and habitat of whatever type of organism he happens to be using for experimental purposes. The writer is fully convinced that naturalistic observation, or field work, should be held alike by naturalists and experimentalists as of equal importance with experimental observation, and should be regarded as an indispensable supplement to the latter. There are naturalists, to be sure, who decry all observation of animal behavior made under experimental conditions, whether within or without the walls of a laboratory, and there are experimentalists who deny the value of naturalistic work, or ignore it. But surely the last decade has furnished abundant proof of the unprofitableness of these attitudes. We propose, so far as is possible, in connection with our laboratory studies of animal behavior, to attempt to unite the naturalistic and the experimental points of view and methods.

The Harvard Psychological Laboratory is particularly fortunate in having the use of a field station in Franklin, New Hampshire, at which naturalistic studies on any organism which will thrive in a temperate climate may be pursued. This station consists of a tract of about one hundred and fifty acres of hill land, of which about half is wooded. The elevation is fourteen to fifteen hundred feet. There are numerous springs and a brook on the tract. Two sets of old farm buildings are available for such needs as arise. This tract, which is constituted by two old farms, was purchased by the writer in the years 1911 and 1912 to serve both as a summer home and as a reservation which might, as seemed desirable, be used for studies in animal behavior

It is proposed that this private field station shall meet two keenly felt needs of the Harvard Laboratory; the one, that of a suitable place for purely naturalistic field work; and the other, that of a similarly suitable place for the conduct of laboratory investigations which cannot well be continued during the summer in Cambridge. We may consider, first, the second of these needs.

There are frequently in progress, in the Harvard Laboratory, researches on heredity or on problems which demand long experimental training, the interruption of which, during the summer vacation, entails serious loss. It is often impracticable to attempt to continue such investigations throughout the summer in Emerson Hall, for even if the investigator is willing to work there, it usually means a serious sacrifice on his part of opportunity for rest and recreation through a change of scenes. The Franklin Field Station, it is hoped, will result in the saving of considerable time to certain investigators, since there it should be possible to continue work uninterruptedly throughout the summer, while at the same time the investigator may profit by the change from city to country and the chance to combine experimental and naturalistic studies in animal behavior with the recreations of a mountainous country.

It is by no means intended that all of the investigations conducted in the Harvard Laboratory shall be transferred to the Field Station. Instead, only a few should or can, to advantage, be so transferred.

But of primary importance, as contrasted with its value as a place for transferred experimental investigations, is the opportunity which the field station offers for naturalistic work. In and about the Cambridge Laboratory, favorable opportunities for training students to observe animals carefully, critically, and at the same time sympathetically, in their native habitats, are rare. And the writer has observed, in many otherwise admirable students of the biological sciences, a tendency toward the acquisition of a narrow minded attitude toward experimental observation, which blinds them to the value of nature-study. It is hoped that at Franklin something may be done for at least a few students of animal behavior to counteract this tendency and to train them to become enthusiastic and reliable naturalists as well as skilled experimentalists.

There is no obvious reason why, at the Field Station, any one

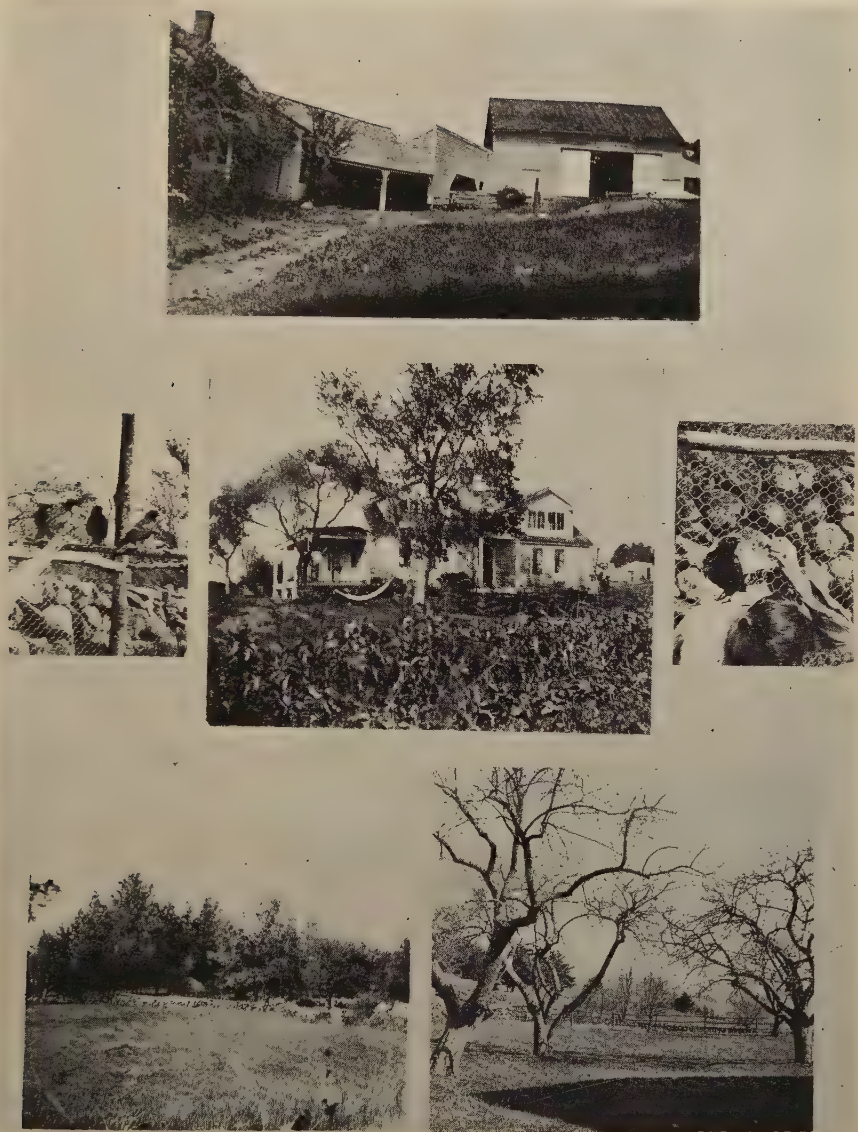

FIGURE 2. Views of the Franklin Field Station for the study of animal psychology.

for later presentation in connection with observations which we hope to make next summer. This paper on the crow initiates a series of contributions from the Franklin Field Station which should, in invaluable ways, supplement our studies from the Harvard Laboratory.

THE BEHAVIOR OF THE CROW, *CORVUS AMERICANUS, AUD.*

CHARLES A. COBURN

From the Harvard Psychological Laboratory and the Franklin Field Station, Franklin, New Hampshire

Many years ago, Henry Ward Beecher remarked that if men were feathered out and given a pair of wings, a very few of them would be clever enough to be crows. This statement represents in a general way the opinion of the mental ability of the crow held by many students of bird life. The literature, both early and late, abounds with anecdotes depicting the intellectual superiority of the crow over other birds.

During the last two decades investigations have been made, by the United States Department of Agriculture and several state boards of agriculture, to determine whether the battle waged by the farmer against the crow is justified. The results of these studies tend to show that the value of the crow to the farmer by its destruction of injurious insects, mice and other rodents, more than compensates for the injury it does to the growing crops. These studies have also provided interesting data on the habits and mental characteristics of the crow. The data, derived in this manner, in no way contradict the general impression. It is, in general, indicated that the crow is very intelligent, supremely cautious and suspicious. Forbush[1] states that, in his opinion, it naturally is neither very cautious nor suspicious, but bold and fearless. Its apparent traits have been acquired by force of necessity. The reason for his statement is that on the Pacific Coast, especially during the early period of settlement, the crows were extremely bold and unsuspicious.

No definite study of the mental ability of the crow was made until 1910, when James P. Porter[2] used three crows in his investigation of intelligence and imitation in birds. His results

[1] Forbush, E. H. Useful Birds and their Protection. Published under the direction of the Massachusetts State Board of Agriculture. 1907.

[2] Porter, James P. Intelligence and Imitation in Birds: A Criterion of Imitation. *Amer. Jour. of Psychology,* 1910, vol. 21, pp. 1-71.

did not put the crow on a higher plane of intelligence than several other birds, especially the English sparrow.

In co-operation with Professor Robert M. Yerkes, an investigation of the intelligence of the crow was begun in June, 1913, at the Franklin Field Station. Work was continued until late September. It is planned to continue the investigation in succeeding summers under the favorable conditions of the station.

The first summer's work included a general study of the habits and development of the bird (to be reported after additional data have been obtained) and a preliminary examination of its ability to discriminate brightnesses, sizes and forms.

It soon became apparent that the adaptation of an apparatus and method to the extremely wary and suspicious nature of the crow was a more difficult task than had been anticipated. This was accomplished after much experimenting with different methods of procedure and many changes in the apparatus. By the time both method and apparatus were fairly well adapted to the characteristics of the crow, the summer was well gone.

Our results are only approximations to the crow's discriminating ability. They are of value, however, in that they indicate certain important tendencies. A comparison of the results obtained during the first weeks with those obtained the last few days clearly shows the effect of improvement in method.

Two crows were used in these experiments. They were taken from a nest near the Field Station on the 6th of June. They were then, probably, about two weeks old. Number 1, a male, was larger and better developed when caught. When full-grown it was larger and bolder and less easily frightened than the female, Number 2.

For two or three weeks after they were caught, the young birds were fed earthworms, with an occasional bit of cooked cereal. Gradually this diet gave way to various kinds of meat, bread soaked in milk, cracked corn soaked in water, and table scraps.

The development, care, and feeding of young crows, will be discussed in a later paper.

When the two crows were about nine weeks old, they were able to fly a short distance and to eat alone. They were so tame that they recognized the voice of the experimenter and would come when called, perch on his arm or shoulder, and eat from

his hand. This friendliness was shown to no other person, and an entire stranger would frighten them very much.

Four other crows were obtained from Pennsylvania, but they were too wild for use in the investigation.

The building, in which the experimenting was done, was divided into two compartments, each 10 feet by 12 feet. One of these served as a roost and feed-room. Adjoining this room was a fly, 24 by 10 by 8 feet high, made of chicken wire. The crows could fly direct from the roost to a perch in the far end of the fly.

The other compartment, which served as an experiment-room, was set off from the feed-room by a partition of chicken wire and a burlap curtain. The curtain could be pulled aside when experiments were not in progress, thus allowing a free circulation of air.

The apparatus used was a modified form of the discrimination-box used by F. S. Breed [3] and later by L. W. Cole [4] in their studies of the reactions of chicks to visual stimuli. The following description is intended to give only the essential points of the apparatus. For a more detailed account, reference may be made to the reports of Breed and Cole.

The entrance-chamber was a movable box 18 by 16 by 14 inches deep. The top, bottom, and three sides were of one-half inch boards. The fourth side was covered with wire netting, one-fourth inch mesh. In each end were openings, 7 inches by 9 inches, with horizontal slide doors.

Leaving the entrance-box, the crow entered the discrimination-chamber. This was 16 by 19 by 13 inches deep. The top was of wire, one-fourth inch mesh. Opening directly into this chamber were two chambers, 18 by 19 by 13 inches deep. The tops of these chambers were of wood as were also the sides and floors. The exit from each of these chambers was 7 inches by 9 inches, with horizontal slide doors. They opened directly into two exit-boxes similar to the entrance-box. The front ends of the stimulus-chambers were formed by a three-stimulus plate-shifter sliding in wooden tracks. For a minute description of this shifter, the reader is referred to the papers of Breed

[3] Breed, F. S. Reactions of Chicks to Optical Stimuli. *Jour. of Animal Behavior*, 1912, vol. 2, pp. 280-295

[4] Cole, L. W. The Relation of Strength of Stimulus to Rate of Learning in the Chick. *Jour. of Animal Behavior*, 1911, vol. 1, pp. 111-124.

and Cole. The stimulus plates used in the experiments on size and form, were the standard plates devised by Yerkes and Watson [5] for their brightness vision apparatus and are described in detail in their paper.

The floor, walls, and top of the discrimination-chamber and the two stimulus-chambers were painted a dark gray. This rendered the two stimulus-chambers alike in every way except with respect to the desired difference in optical stimuli, namely, that of brightness, size, or form. Care was taken throughout the work to see that this was the only means by which the crow could choose the correct path.

The exit doors were operated by a system of cords. A curtain was suspended from the ceiling at the rear of the apparatus. The experimenter, standing behind the curtain and looking through a small peep-hole, could observe the behavior of the crow while in the apparatus and open and close the exit-doors without being seen by the crow.

Late in the summer, two swinging gates of wire were suspended between the discrimination-chamber and the two stimulus-chambers. These gates also were operated by cords. At the beginning of a test they were drawn up to the ceiling of the discrimination-chamber. The purpose of these gates was to prevent the crow from returning into the discrimination-chamber after it had made a wrong choice.

During the experiments on brightness discrimination, the apparatus faced a north window. With the beginning of the tests of size discrimination, it was shifted to face a larger south window. In this position, it remained during the rest of the season.

The ability of the crow to detect a slight change in the situation, together with its wary and suspicious nature, made it impossible to choose a method of procedure at the beginning and to adhere to it rigidly throughout the period of work. The method used at the beginning was evolved during the preliminary trials, when the first indications were received of what the crow might reasonably be expected to do. Various changes were made in this initial method until a reasonably satisfactory one had been developed.

[5] Yerkes, R. M., and Watson, J. B. Methods of Studying Vision in Animals. *Behavior Monographs*, 1911, vol. 1, no. 2, p. 23.

For several days previous to the first preliminary series, the crows were compelled to enter the discrimination-chamber in order to get their food. For this purpose the apparatus was placed before a small door in the partition separating the feed-room from the experiment-room. At first, the pan containing the food, was placed just inside the entrance door. Then, gradually, it was placed farther back until the crows were required to go through the discrimination-chamber, and the one or the other of the stimulus-chambers, into the exit-boxes. After a few days, they did this with no apparent fear.

The first preliminary tests were given on July 16th. The crows were then about nine weeks old. The standard stimulus plates had been removed from the stimulus shifter, leaving square openings, 12 cm. by 12 cm. Opal flashed glasses were placed in the slides immediately before these openings, so the illumination of the two chambers was the same.

The apparatus was adjusted with the entrance-box before the small door in the partition between the feed-room and the experiment-room. When one of the crows had entered this box to get the bit of food placed therein, both doors were closed and the entrance-box was then placed before the entrance to the discrimination-chamber. The door leading to the discrimination-chamber next was opened and the crow allowed to enter. The exit doors being open the crow could proceed to one of the exit-boxes and obtain food. The exit and entrance-boxes were now exchanged and the crow given another trial.

Both crows were much frightened by being confined in the entrance and exit-boxes. After two days, with nine such trials, they became somewhat calmer during the experiments. The exit doors were now closed and the crows allowed to enter the discrimination-chamber, go to one of the stimulus-chambers and there wait until the exit door was opened. This new situation, especially the opening of the exit door, frightened them as much as being shut in the entrance or exit-boxes had at the beginning. In the first trial they could not be induced to enter the discrimination-chamber until the exit doors were opened as before. However, after eight trials with the doors closed, they had lost much of their fear. In these seventeen trials, Number 1 went eleven times to the right and six times to the left. Number 2 went every time to the right.

When the crow chose the correct path, it was always rewarded with a bit of food,—a small piece of mouse, frog, or other meat. If it chose incorrectly, it received no food and was required to remain three or four minutes in the exit-box, which had been previously darkened by a cloth thrown over the wire side. The dislike of crows to remain in a darkened chamber was utilized also by the gradual darkening of the entrance-box when the crows hesitated too long before entering the discrimination-chamber at the beginning of a test. This never failed to cause them to leave immediately. There were, therefore, at least two motives for correct choice, namely, the desire for food and the dislike of the darkened box. The latter can be considered a constant factor, for they reacted to the darkened box as strongly at the end of the summer as they did at the beginning.

Care was taken throughout the experiments to keep the factor of hunger constant. It was impossible to do this at all times, and it is highly probable that the results in many cases were materially affected by the change in this factor.

In the beginning, two series of five tests each were given per day. The times for the beginning of these series varied slightly, but as a rule they were 7:30 A. M. and 1:00 P. M. The crows, with this number of tests, would still be hungry at the end of the series, so the number of tests per series was raised to ten and the amount of food given at the end of each correct choice was lessened. It soon became apparent that the crow, in this case, was confined too long. After the seventh or eighth test, it usually busied itself more with getting out of the apparatus than with choosing the correct path in order to get food. On this account, three series, (7:30 A. M., 12:00 M. and 4:00 P. M.), of eight tests each were given per day. Finally the number of trials in each series was changed to five, and this seemed to be the best solution of the problem, as the crows were sufficiently hungry three times a day to be eager to get food. In the majority of cases, they were still hungry at the end of a series. The time required for the five tests was rarely over ten minutes, and the crows, as a rule, did not become restless in this time.

As a rule, one crow was given all the trials of a series before the other was caught. In a few series, the crows were given alternate tests. This was not conducive to the best results, for the crow, waiting in the entrance-box until the other completed

the test, would become so restless that in many cases it would begin to throw itself against the woven wire side of the box. By the time its turn came, the desire to escape from the box had entirely overcome the desire for food, and, as a result, it would rush through the test and recommence its struggle to free itself. If, by chance, it made a correct choice, the food would not be noticed.

The results of each series of tests were kept on record sheets similar to those used by H. C. Bingham[6] in his study of the perception of size and form in the chick. In addition to a record of the correct and incorrect choices, the time required for the choice and a sketch of the path of the crow were also recorded.

In the study of brightness perception, the apparatus remained as in the preliminary series except that the stimulus areas of the stimulus-chambers differed in intensity. This difference was obtained by the use of more or less opaque substances, namely, black cardboard, milk glasses, and paper. These were placed over the opal flashed glass of one of the stimulus areas. The slides, which held the plates of opal flashed glass before the stimulus areas, were large enough to admit also the cardboard, milk glasses, or sheets of paper.

Black cardboard was first used. Since it allowed no light to pass, the illumination of the stimulus area before which it was placed was practically zero. The crows, in the trial series, had become partially accustomed to stimulus areas of an intensity produced by light passing through but one thickness of opal flashed glass. Consequently in the brightness experiments, they avoided the darkened chamber. The chambers were darkened in no regular order, but in ten or twenty tests, one chamber would be darkened as many times as the other.

After fifteen tests with each crow, the cardboard was exchanged for two milk glasses, then later for one milk glass and finally for one sheet of paper. The difference in the intensity of the two areas in this last case was comparatively slight. With care it could be distinguished by the human eye.

Table 1 shows the results of these tests.

---

[6] Bingham, H. C. Size and Form Perception in *Gallus domesticus*. *Jour. of Animal Behavior*, 1913, vol. 3, no. 2, pp. 65-113.

TABLE 1

Intensity Discrimination

Date	No. of tests	Correct choices Crow No. 1	Correct choices Crow No. 2
Conditions of Discrimination			
Cardboard and opal flashed glass—Opal flashed glass			
July 19	5	5	5
" 19	5	4	5
" 20	5	5	5
Two milk glasses and opal flashed glass—Opal flashed glass			
July 21	5	5	5
" 21	5	5	5
" 22	5	4	5
One milk glass and opal flashed glass—Opal flashed glass			
July 22	5	5	2
" 23	5	3	3
" 23	5	4	4
" 24	5	4	4
" 24	5	5	4
" 25	5	3	4
" 25	5	4	5
" 26	5	5	5
" 27	5	4	5
" 28	5	5	5
" 28	5	5	4
One sheet of paper and opal flashed glass—Opal flashed glass			
July 29	5	4	3
" 30	5	5	3
" 30	5	5	3
" 31	5	5	3
" 31	5	5	4
Aug. 1	5	5	4
" 1	5	5	5

These results are but roughly indicative of the crows' ability to distinguish differences in illumination. Accurate measurements of the birds' visual acuity was not the aim of our experiments.

The chief value of these experiments on the discrimination of intensity is the demonstration of the ease with which the crow is able to adapt itself to experimental conditions and to solve accurately one variety of problem.

With the beginning of the experiments on size discrimination, the apparatus was so shifted that the front end was immediately before a large south window. In this position it remained during the season. The only other change was the insertion of the

standard stimulus plates in the stimulus shifter. Difference in the illumination of the stimulus areas was eliminated.

A 5 centimeter [7] circle versus a 2 centimeter [7] circle was chosen for the beginning of this study. The correct exit was indicated by the larger circle.

This change in the conditions of discrimination naturally threw the crows into confusion. They refused to enter the discrimination-chamber unless forced to do so by the darkening of the entrance-box. If this were done, they would pass to and fro before the two stimulus-chambers, but they would not enter far enough into either of them for the exit doors to be opened. The series of the first two days had to be interrupted on account of the crows' fright. On the third day no attempt was made to work. During the day the crows were fed somewhat less than the usual amount of food. The next morning (August 5th), they were tried with a 9 centimeter circle versus a 5 centimeter circle. By this change the illumination of the stimulus-chambers was made to approximate that to which the crows had become accustomed in the experiments on the discrimination of intensity. Their hunger, on this day, was great enough to overcome in large measure their fright. The results of this, and the remaining series on size discrimination are given in Table 2.

After one series with the 9 centimeter versus the 5 centimeter circle, a 2 centimeter circle was substituted for the 5 centimeter circle. The crows' behavior now became practically normal. The only significant difference from previous reactions was a greater hesitation in choosing. Before finally entering a chamber, they would often pass to and fro several times before the two stimulus-chambers, again and again starting to enter one chamber only to back out and go to the other. As appears in the table, crow no. 1 made twenty correct choices in succession, while crow no. 2 succeeded in choosing correctly eighteen times in twenty. This sudden return of calm and controlled reaction and the high percentage of correct choices, were due probably to the fact that the illumination of the stimulus-chambers through the 9 centimeter and the 2 centimeter circles was closely similar to that in the experiments on intensity discrimination.

[7] Stimulus plates will be designated by the diameter or the side.

It seems probable that the birds were simply choosing the more highly illuminated stimulus-chamber, which, in every case, was also the one presenting the larger stimulus area. That they did not continue to use this cue is proved by experiments in which the large stimulus area, and irregularly the small one also, were darkened by placing one thickness of milk glass over the opal flashed glass. This enabled the experimenter in some tests to present two stimulus areas differing in size and intensity of illumination. Now the chamber illuminated by the larger circular area was the more intense, and now the one illuminated by the smaller area. Had the crows attempted to depend upon the illumination of the chambers, or on the relative intensities of the stimulus areas, instead of on their size, they certainly would have been confused. As a matter of fact, the change influenced markedly neither their behavior nor their percentage of correct choices.

The experiments on the perception of size were continued for twenty-five days. The results (Table 2) show that the crows

TABLE 2

PERCEPTION OF SIZE

Date	No. of tests	Correct choices Crow No. 1	Crow No. 2
	Conditions of Discrimination		
	5 centimeter—2 centimeter circle		
Aug. 2	Crows frightened. Abandoned series.		
" 3	Crows frightened. Abandoned series.		
	9 centimeter—5 centimeter circle		
Aug. 5	5	3	4
	9 centimeter—2 centimeter circle		
Aug. 6	10	10	8
" 6	10	10	10
	5 centimeter—2 centimeter circle		
Aug. 7	10	10	10
" 7	10	9	10
" 8	10	9	9
" 8	10	7	10
" 9	10	5	9
" 9	10	10	9
	5 centimeter—3 centimeter circle		
Aug. 10	10	8	9
" 11	10	8	7
" 11	10	9	10

TABLE 2—*Continued*

Date	No. of tests	Correct choices Crow No. 1	Crow No. 2
		Conditions of Discrimination	
		3 centimeter—2 centimeter circle	
Aug. 12	10	9	7
" 13	8	4	4
" 13	10	6	7
" 13	8	8	5
" 14	8	6	6
" 15	7	6	6
" 15	9	7	8
" 15	8	5	5
" 16	8	7	5
" 16	8	8	8
" 16	8	6	5
" 17	8	6	4
		5 centimeter—3 centimeter circle	
Aug. 17	8	8	6
" 18	8	8	8
" 19	5	3	3 (Left habit)
" 19	6	4	6
" 20	10	4 (Left habit)	8
" 20	10	8	9
" 20	10	7	10
" 21	10	9	10
" 21	10	5 (Left habit)	9
" 21	5	3	5
" 22	8	7	7
		6 centimeter—3 centimeter circle	
Aug. 22	8	8	7
		5 centimeter—3 centimeter circle	
Aug. 22	8	6	8
" 23	8	3 (Left habit)	8
" 23	8	6	7
" 24	10	9	6
" 24	10	10	9
" 25	10	9	9
" 25	10	9	9

improved surprisingly little with practice. The percentage of correct choices with the 5 centimeter versus the 3 centimeter circle was as low during the last few days of the training as it was on August 10th and 11th when they were first required to distinguish between these circles.

Throughout these experiments, the behavior of the crows while working was very erratic. Some days they worked slowly and carefully. Sudden noises, such as those caused by the opening or closing of an entrance or exit door, did not greatly

disturb them. The results on these days of calm steadiness, as a rule, showed an increase in the number of correct choices. On other days, their behavior would be practically the opposite. While still in the entrance-box they would walk impatiently to and fro before the woven wire side of the box. When the entrance door was opened, they would often start several times to enter only to turn back into the entrance-box. When they finally did enter, they would rush to one of the exit doors, and, in a crouching attitude, wait until it was opened. On these days, great care had to be taken in opening and closing the doors for an unusual noise or sudden movement would greatly increase their excitement. During this behavior they were very likely to develop a position habit. Series, in which this excited behavior resulted in a considerable number of incorrect choices, have been noted in the tables.

The ability of the crow to pass directly from one set of circles to another with no great difference in the number of correct choices (see Table 2), was further tested by a series of experiments, the results of which appear in Table 3.

In these experiments, the attempt was made to determine whether the crows were reacting to a certain specific stimulus, or whether they were reacting to it because of its relation to another stimulus. For instance, if the 6 centimeter and the 4 centimeter circles were presented, and the crow trained to react positively to the 6 centimeter circle, would it continue to do so when the 6 centimeter circle was presented with a 9 centimeter circle, or would it, instead, choose the larger area in each instance?

As in the preceding series the crows were trained to choose the larger of two circles. When they had gained the ability to choose correctly, they were given ten trials with a different pair of circles. During these ten trials, they were rewarded after each test, regardless of the correctness or incorrectness of the reaction. A reaction was considered correct if the crow chose the larger circle. These series are designated, in Table 3, "relative reactions." The training series which preceded the relative series of August 26th are given in Table 2.

The results of these experiments indicate fairly clearly the relativity of the crows' reactions. Especially is this true of crow no. 1. For example, on August 24th and 25th, when the

3 centimeter circle was presented with the 5 centimeter circle, the crow reacted to the 3 centimeter circle thirty-seven times negatively and three times positively. On August 26th, the 3 centimeter circle, displayed with the 2 centimeter circle, was reacted to positively in every case. The results for crow no. 1 with the 6 centimeter circle when displayed with the 4 centimeter and the 9 centimeter circles, on August 26th and 27th, were almost as decisive.

TABLE 3

Reactions to Relative Sizes of Circles

Date	No. of tests	Correct choices Crow No. 1	Crow No. 2
	Relative reactions, 3 centimeter—2 centimeter circle		
Aug. 26	5	5	5
" 26	5	5	3
	Training series, 6 centimeter—4 centimeter circle		
Aug. 26	10	7	9
	Relative reactions, 9 centimeter—6 centimeter circl		
Aug. 27	5	4	2
" 27	5	5	3
	Training series, 6 centimeter—4 centimeter circle		
Aug. 27	8	2	5
" 28	10	6	8
" 28	8	5	3 (Righ habit)
" 29	5	4	4
" 29	5	4	3
" 29	6	5	5
	Relative reaction, 3 centimeter—2 centimeter circle		
Aug. 30	5	5	2
" 30	5	5	4
	Training series, 6 centimeter—4 centimeter circle		
Aug. 30	5	5	2
	Relative reactions, 9 centimeter—6 centimeter circle		
Aug. 31	5	2	4
" 31	5	4	3

Only one day intervened between the conclusion of the tests of the relativity of the reactions and the beginning of experiments to determine the ability of the crow to distinguish circles from triangles, squares and hexagons.

With the beginning of this study of form perception the experimenter became more convinced than ever that the results, obtained in the previous experiments, did not truly indicate the

crows' intelligence. A new form of reaction now developed. When either of the crows had made an incorrect choice and the exit door was opened, showing a dark exit-box, instead of entering as they hitherto had done, they would whirl about and quickly go to the other exit and there wait, even for five or ten minutes, until the door was opened. This behavior naturally tended to lower the percentage of correct choices.

The experimenter first tried to overcome this difficulty by having the exit-box illuminated until they had entered it. Crow no. 2 would always enter the box under these conditions, but crow no. 1, after a few trials, refused to enter either box unless there was a bit of food in view.

To meet this difficulty, the gates, described on page 188, were constructed. When the crow entered the wrong stimulus-chamber, the exit door was opened and at the same moment the gate between that chamber and the discrimination-chamber was dropped, thus preventing the crow from escaping to the other exit. The dropping of the gate tended to frighten them somewhat, so they always quickly entered the exit-box, which was again darkened as in the early experiments. The effect of this improvement in the apparatus on the behavior of the crows appears in the results of Table 4.

The crows had been given one hundred and six tests for their ability to distinguish a 6 centimeter circle from an 8.081 centimeter triangle. During these trials no appreciable increase in the percentage of correct choices had been made. Immediately after the gates were brought into use, improvement commenced and thereafter the majority of the choices were correct. Crow no. 2 did not make quite as high a percentage of correct reactions as did crow no. 1. This was probably because no. 2 seemed to be more frightened by the dropping of the gate. If an incorrect choice was made early in a series, there was a tendency, on the part of no. 2, to avoid that stimulus-chamber during the remainder of that series.

The 6 centimeter circle, the 8.081 centimeter triangle, the 5.317 centimeter square, and the 3.29 centimeter hexagon are of equal area. The last thirty tests were with figures unequal in size. The 6 centimeter and the 9 centimeter circles each possess a greater area than the 3 centimeter hexagon, whose area, in turn, is almost twice as great as that of the 3 centimeter circle.

TABLE 4

DISCRIMINATION OF FORM

Date	No. of tests	Correct choices	
		Crow No. 1	Crow No. 2
	Conditions of Discrimination		
	6 centimeter circle—8.081 centimeter triangle		
Sept. 2	6	5	3
" 2	5	4	3
" 3	5	3	4
" 3	5	4	3
" 3	5	4	3
" 4	5	4	2
" 4	5	5	2
" 4–8	45	39	32
" 8	5	5	2 (Right habit)
" 8	5	3	4
" 9	5	3	4
" 9	5	3	5
" 10	5	3	1 (Left habit)
" 10	5 (Began using gates)	3	5
" 11	5	5	4
" 11	5	5	5
" 11	5	3	5
" 12	5	5	4
" 12	5	5	5
" 12	5	5	5
	6 centimeter circle—8.081 centimeter triangle (Inverted)		
Sept. 13	5	5	5
	6 centimeter circle—5.317 centimeter square		
Sept. 13	5	5	5
" 13	5	5	5
" 14	5	5	3 (Left habit)
" 15	5	5	5
	6 centimeter circle—4.243 centimeter square		
Sept. 15	5	5	5
" 15	5	4	5
" 16	5	5	5
	6 centimeter circle—3.29 centimeter hexagon		
Sept. 16	5	4	4
	6 centimeter circle—3.00 centimeter hexagon		
Sept. 16	5	5	5
" 17	5	5	4
	3 centimeter circle—3.00 centimeter hexagon		
Sept. 17	5	5	3
" 18	5	5	2 (Left habit)
	9 centimeter circle—3.00 centimeter hexagon		
Sept. 18	5	5	4
" 18	5	5	5

The intensities of the stimulus areas and the general illumination of the chambers were varied in these tests by the use of milk glasses as described on page 194. The only visual factor which was constant during the thirty trials, was that of form. It is evident, therefore, that this was the cue which enabled crow no. 1 to make a perfect record in these series.

Lack of time prevented further work on the perception of form. The last two days of work were devoted to a further study of size discrimination. The purpose was to obtain, if possible, more conclusive evidence of the crows' ability to distinguish sizes, and, incidentally, to learn if the improvement in the method (introduction of gates) would increase the percentage of correct reactions to differences in size.

Thirty tests were given, the results of which appear in Table 5. During the first series, the crows appeared to be confused by the sudden change in the problem presented to them. They worked rather slowly and quietly, but their choices were not made with the usual definiteness. It was evident that they (especially crow no. 1), did not clearly appreciate what was required of them.

TABLE 5

DISCRIMINATION OF SIZE

Date	No. of tests	Correct choices Crow No. 1	Crow No. 2
	Conditions of Discrimination		
	5 centimeter—3 centimeter circle		
Sept. 19	10	4	7
" 19	5	5	4
	5 centimeter—4 centimeter circle		
Sept. 19	5	5	5
	5 centimeter—4.5 centimeter circle		
Sept. 20	5	4	4
" 20	5	5	5

In the second series, the indefiniteness and hesitation in their behavior were lacking. In every case no. 1 went quickly and directly to the correct exit. Crow no. 2 made a mistake in the first test. Its decisions, however, were made clearly and definitely thereafter. This clear-cut, decisive type of reaction continued, with both crows, during the remaining tests, even when the discrimination was between the 5 centimeter and the

4.5 centimeter circles. If quickness of choice can be taken as a measure of the ease of discrimination, it is probable that the crows are capable of distinguishing much smaller differences.

The crow deserves its reputation. It is an exceptionally interesting subject for the behaviorist and worthy of his greatest skill. As has been indicated earlier in this report, it is planned to observe systematically crows at the Franklin Field Station, both in the field and in the laboratory, in order that a reasonably complete and reliable description of their behavior may be given. Because of the division of labor among a number of observers, it will be necessary to publish reports from season to season instead of reserving all materials for a monograph. The present paper is indicative of some of the chief characteristics of the bird, and suggestive of experimental difficulties. Another season should prepare us to report on the habits, instincts, and development.

SOME RELATIONS BETWEEN RHEOTAXIS AND THE RATE OF CARBON DIOXIDE PRODUCTION OF ISOPODS

W. C. ALLEE
Thompson Biological Laboratory, Williams College
AND
SHIRO TASHIRO
Laboratory of Biochemistry and Pharmacology, the University of Chicago

For several years one of us has been working upon an analysis of the rheotactic reaction of the isopod, *Asellus communis*, Say. In the course of this work it became evident that certain conditions known to affect animal metabolism likewise regularly affected the rheotactic reaction of isopods. Thus it was found that low oxygen tension, high carbon dioxide tension, chloretone, potassium cyanide, lowered temperature, sudden extreme increase of temperature, starvation, and fatigue decreased the percentage of positive rheotactic responses given. On the other hand caffein, increased oyxgen tension, and a gradual increase of temperature had the opposite effect. (Allee, '12, '13.)

When the rate of metabolism of isopods was determined by their resistance to potassium cyanide (Child, '13, '13a; Allee, '14; also page 206.) isopods giving a high percentage of positive rheotactic responses in a circular current had the highest rate of metabolism. Those with a high per cent. of negative responses were second, while those with a low positive response and with either the negative or indefinite reaction dominating had the lowest rate of metabolism.

For a number of years the other of us has been working upon a method for determining with analytical accuracy the minute amounts of carbon dioxide given off in the metabolism of nerve fibers. (Tashiro, '13, '13a, '14.) The apparatus devised will detect and measure with accuracy 0.000,000,1 gram of carbon dioxide.

For those who are not familiar with the new method for determining carbon dioxide we may say that the quantitative method depends upon determining the minimum amount of gas

which will give the first precipitate of barium carbonate when introduced into a chamber in which a perfectly clear drop of barium hydroxide is exposed. It was previously found by work with known amounts of very dilute carbon dioxide that the minimum amount of carbon dioxide which gives the first precipitate is 0.000,000,1 gram. Thus, by determining the minimum number of cubic centimeters of a gas from a respiratory chamber of known volume, we can calculate very accurately the amount of carbon dioxide given off by the tissue or animal under observation.

The details of the method are as follows: An animal is left in the respiratory chamber (15 cc. capacity) for a respiration period of ten minutes. Then this air is driven into a gas pipette. After cleaning and washing the apparatus one cubic centimeter of this gas is introduced into the barium hydroxide chamber but gives no precipitate; .25 cc. more is introduced with no result; .25 cc. more gives a precipitate. The total volume introduced, 1.5 cc. is the minimum volume that will give the first precipitate. Since 0.000,000,1 gm. of carbon dioxide is the minimum amount which gives the first precipitate, it is certain that 1.5 cc. of respired air must contain 0.000,000,1 gm. of carbon dioxide. The total respiratory chamber must have contained $\frac{15}{1.5}$ x 0.000,000,1 or 10 x 10^{-7} grams carbon dioxide.

Not all of the work to be reported in this paper was done in this detailed quantitative manner since in some cases only comparative results were needed. For the comparative work a piece of apparatus called a Biometer[1] (Tashiro, '13.) was used. This consists essentially of two chambers of equal size which are prepared for a determination in exactly the same manner and the animals to be tested for relative carbon dioxide production are inserted. At the start each chamber contains a perfectly clear drop of barium hydroxide. The chamber which first shows a precipitate of barium carbonate and which later shows more precipitate evidently has had carbon dioxide produced at a higher rate than the other chamber. Hence it is easy to find which of two isopods is producing the greater amount of carbon dioxide.

[1] Quantitative determinations can also be made with the Biometer by using one chamber as a respiration chamber and the other for the determination.

THE PROBLEM

With this more refined method of obtaining an insight into the relation between physiological states and animal behavior the following three lines of inquiry were prosecuted during the time at our disposal at Woods Hole during the summer of 1913:

1. What is the relation between the rate of carbon dioxide production of isopods and their resistance to relatively strong solutions of potassium cyanide?

2. What is the effect of the calcium ion upon carbon dioxide production and rheotaxis in isopods?

3. Is there a relationship between the variation in carbon dioxide production and the rheotactic reaction of isopods?

THE STOCK

Isopods from a series of collections from small fresh water ponds near Woods Hole, Massachusetts, were used in these experiments. They were all *Asellus communis*, Say, and were about half grown. The isopods came from silt and debris bottomed ponds and were kept under comparable conditions in the laboratory.

METHODS

The isopods were tested for their rheotactic reaction in a circular current the bottom of which was covered with wax. The responses of an individual isopod for ten successive minute reaction periods were taken as a fair indication of the rheotactic tendencies of the animal. The isopods were judged to give a positive reaction when they went against the current for over half of the minute's reaction period. They were considered to give a negative reaction when they moved with the current for over half of their minute's trial and indefinite when their movements gave no indication of being regulated by the direction of the current. The approximate distance covered by each reaction was recorded and will be found in a standardized form in the tables under the head of efficiency in the current. In general the movements of highly positive isopods are more vigorous than those of negative isopods, which in turn are more vigorous than those giving an indefinite reaction. (For further details see Allee, '13.)

When the carbon dioxide output was to be tested the isopod was dipped into water free from carbon dioxide, dried momen-

tarily on filter paper and placed on a cover glass with no water added except that which clung to the animal. An amber ring about three millimeters high was placed around the isopod and this was covered with wire gauze to prevent extended movement of the animal while in the respiration chamber.[2] This precaution was the more effective since isopods are strongly positively thigmotactic and will rest quietly for extended periods when they are able to place their bodies in an angle of their container.

When comparisons were made in the Biometer, isopods of approximately the same size were selected in order to guard against a greater production of carbon dioxide due to greater mass. The isopods were left in the respiration chambers for only ten minutes during the quantitative work but in the qualitative results, tested in the Biometer, the isopods were left as long as thirty minutes. The fact that isopods survived nine daily tests and showed no ill effects of the handling demonstrates there is little danger to the animal in such treatment.

THE RELATION BETWEEN CARBON DIOXIDE PRODUCTION AND RESISTANCE TO POTASSIUM CYANIDE

The work upon the relation between carbon dioxide output and the resistance of isopods to potassium cyanide was qualitative only and was carried on to ascertain whether or not the resistance of isopods to the cyanide is a safe index of their metabolic activity. Child ('13, '13a) found that in Planaria the susceptibility of animals or pieces of animal to 0.001 mol. solution of potassium cyanide varied in general with the rate of metabolism. Estimation of carbon dioxide production on individuals and pieces (of the same species) made at Dr. Child's request by Tashiro with the aid of his Biometer showed that carbon dioxide production ran parallel with susceptibility to potassium cyanide, and so afforded a confirmation of Child's conclusion concerning the relation between susceptibility and the rate of metabolism.

[2] We appreciate the roughness of this method for checking spontaneous muscular movement, but it was out of consideration for us to devise an automatic recorder for bodily activity such as is necessary in order to make accurate metabolism experiments with mammals. The principal source of error in determining the amount of carbon dioxide given off by isopods lies in the fact the spontaneous muscular movements were not under complete control. With the device described above and by constant, careful observation with a hand lens of the animal during the experiment, we convinced ourselves that we had sufficient control of the movements of the animals to answer the needs of our experiments.

Allee has conducted a series of tests to find whether or not Child's cyanide resistance method would apply to isopods and has found decided evidence that the application is possible. (Allee, '14.) As a final check upon this work we repeated with isopods the tests of the relation between carbon dioxide production and cyanide resistance that had been made earlier for Planaria.

The detailed method of procedure was as follows: Two easily distinguished isopods of equal size, whose rheotactic reaction had been previously tested by Allee, were placed in the Biometer by Tashiro and the relative speed of carbon dioxide output was determined. Immediately upon the removal of the

TABLE 1

Showing the relation between the rheotactic reaction, carbon dioxide production and resistance to 0.001 mol. potassium cyanide. The carbon dioxide output was compared in the biometer and the total reactions of two animals thus compared are shown in each horizontal division of the table.

Isopod No.	Rheotactic reaction in percentage of total number of trials				Efficiency in the current	Carbon dioxide output compared	Survival time in .001 mol. KCN. in hours and minutes	Sex	Length in mm.
	+	—	∞	0					
92 89	60 0	20 70	20 30		2.1 2.0	more less	2:10 3:10	♂ ♂	6.5 6.0
86 87	100 100	0 0	0 0		2.1 2.2	more less	2:00 2:30	♂ ♀	5.0 7.0
90 91	80 80	10 10	10 10		2.1 2.0	more less	2:00 2:30	♂ ♀	6.5 5.5
95 94	100 20	0 80	0 0		2.6 2.2	more less	5:30* 4:45	♂ ♂	7.0 5.0
30 169	70 40	20 20	10 40			more less	2:20 3:10	♂ ♂	4.5 5.0
84 171	10 60	0 40	40 0	50		less more	2:55 1:35	♂ ♂	6.0 5.5

* See discussion, page 207.

isopods from the respiration chamber they were placed in an Erlenmeyer flask in 0.001 mol. solution of potassium cyanide and their survival time was ascertained by Allee. It should be noted that the experimenter on the determination of the carbon dioxide output was ignorant of the behavior of the animals, thus eliminating any prejudice for the determinations. The results of experiments of this character are shown in table 1.

The table shows that in ten of the twelve isopods tried the evidence from the survival time ran parallel with that of the carbon dioxide production, that is, the isopods giving the more carbon dioxide had the shorter survival time in the cyanide. The table also shows that where there was a difference in the rheotactic reaction of the animal tested, the more carbon dioxide was given by the isopod that gave the higher percentage of positive rheotactic reactions. (Cf. page 213; also Allee, '14.) In the case of isopods No. 94 and 95 where the isopod that gave off less carbon dioxide lived a shorter time in the cyanide the experimental records show that No. 95 moved more in the respiration chamber than did No. 94 and also that it was two millimeters longer. Either of these factors might account for the discrepancy. If the potassium cyanide resistance in this case is taken as the true index of the metabolism it will be noted that the animals living longer, i.e., having the lower rate of metabolism gave the highest percentage of positive rheotactic reactions. This apparent contradiction will be discussed later (page 211).

Since in 83% of the cases tried the carbon dioxide production tallied exactly with the resistance to potassium cyanide and in the other 17% of the cases the apparent exception is capable of reasonable explanation, it seems safe to conclude that so far as carbon dioxide production is concerned the resistance of isopods to potassium cyanide is a safe index of the metabolic activity of the animals.

THE EFFECT OF THE CALCIUM ION UPON RHEOTAXIS AND CARBON DIOXIDE PRODUCTION

In connection with experiments on irritability Tashiro has studied the effects of inorganic salts upon tissue metabolism. Whatever the mechanism of the effect of such salts on tissues

TABLE 2

Showing the effect of calcium chloride upon carbon dioxide production and rheotaxis in isopods. The survival time in potassium cyanide is added for comparative purposes. The isopods were first tested for rheotaxis, then two of approximately the same size were taken for determination of their carbon dioxide output in the biometer. The one of these that gave the least carbon dioxide was taken as a control, its rheotactic reaction was again tested and it was allowed to stand in water to which it was accustomed while the other was treated.

The second isopod, the one giving the most carbon dioxide, was placed in a 0.16 mol. solution of calcium chloride until the positive rheotactic tendency was markedly decreased. Immediately afterward the carbon dioxide production of the two was again compared in the biometer.

Isopod No. 30	Isopod No. 169
Rheotaxis test, 11:55 A. M. Temp. 20 50%+, 50%—; Efficiency, 2.1 Tested in Biometer 1:47-2:00 P. M. Temp. 23.5 Less CO_2 than No. 169 Rheotaxis test 2:00 P. M. 70%+, 20%—, 10%∞; Efficiency, 2.25	Rheotaxis test, 12:25 P. M. Temp. 20 90%+, 10%—; Efficiency, 2.1 Tested in Biometer 1:47-2:00 P. M. Temp. 23.5 More CO_2 than No. 30 Put in 0.16 Mol. $CaCl_2$ 2:05 P. M. Rheotaxis test 2:07 P. M. 80%+, 20%— Efficiency, 1.6 Rheotaxis test 2:27 P. M. 40%+, 20%∞, 40%o; Efficiency, .95 Taken from $CaCl_2$ 3:43 P. M. In $CaCl_2$ 36 minutes
Tested in Biometer 3:44-3:57 P. M. More CO_2 than No. 169 Survival time in 0.001 Mol. KCN 2 hours, 20 minutes ♂, 4.5 mm. long	Tested in Biometer 3:44-3:57 P. M. Less CO_2 than No. 30 Survival time in 0.001 Mol. KCN 3 hours, 10 minutes ♂, 5.0 mm. long
Isopod No. 171	**Isopod No. 84**
Rheotaxis test 12:25 P. M. Temp. 20 10%+, 90%—; Efficiency, 2.4 Tested in Biometer 2:49-3:05 P. M. Little CO_2 given off Less CO_2 than No. 84 Rheotaxis tested 3:50 P. M. 60%+, 40%—; Efficiency, 2.0	Rheotaxis test 12:00 M. Temp. 20 30%+, 60%—, 10%∞; Efficiency, 2.6 Tested in Biometer 2:49-3:05 P. M. Little CO_2 given off. More CO_2 than No. 171 Put in 0.16 Mol. $CaCl_2$ 4:02 P. M. Rheotaxis tested 4:07 P. M. 10%+, 40%∞, 50%o; Efficiency, 0.9 Taken from $CaCl_2$ 4:27 P. M. In $CaCl_2$ 25 minutes
Tested in Biometer 4:35-5:12 P. M. More CO_2 than No. 84 Survival time in 0.001 Mol. KCN 1 hour, 35 minutes ♂, 5.5 mm. long	Tested in Biometer 4:35-5:12 P. M. Less CO_2 than No. 171 Survival time in 0.001 Mol. KCN 2 hours, 55 minutes ♂, 6.0 mm. long

may be, it was clearly proven (Tashiro, '13), that inorganic salts which affect physiologic states of the nerve equally modify metabolism as measured by the carbon dioxide production. With Dr. Lingle[3] he has further extended the study of the effects of calcium and sodium ions upon tissue metabolism upon isolated pieces of heart tissue of turtles.

Allee[3] has spent considerable time upon the effects of certain inorganic salts upon the rheotactic reactions of isopods and found among other results that calcium chloride caused animals that were highly positive to a water current to become much less positive. That the calcium rather than the chlorine ion is responsible for these results is shown by tests with a number of other inorganic chlorides some of which increase while others decrease the positiveness of the rheotactic reaction of isopods.

From his work on tissue metabolism Tashiro suggested that the calcium chloride in some way caused a decrease in the metabolic activity of the isopods. In order to test this the crucial experiments were made the results of which are exhibited in table 2.

Although only two comparisons were made yet the results are so diagrammatic and are so fully in accord with the previous experience of both authors that they may fairly be taken as giving a truthful picture of the conditions under consideration.

In brief the experiments were as follows: Two isopods of approximately the same size were tested for their relative rate of carbon dioxide production in the Biometer. The isopod having the lower rate of carbon dioxide output was taken as a control and was again tested for the rheotactic reaction and then left in conditions to which it was acclimated while the other was treated. The second individual, which had the higher rate of carbon dioxide production was placed in a 0.16 mol. solution of calcium chloride until the tendency to give a positive rheotactic reaction was markedly reduced. Then the rate of carbon dioxide production of the two was again tested in the Biometer.

In both pairs tested the isopod with the higher rate of carbon dioxide production at the first test in the Biometer had also given the higher percentage of rheotactic responses, but after being treated with calcium chloride for 25-36 minutes it came to be less positive in its rheotactic reaction, and also gave less

[3] Unpublished results.

carbon dioxide and was less susceptible to potassium cyanide than the control individual. In other words the calcium chloride (0.16 mol.) decidedly decreased the rate of metabolism of the isopods and also reduced their tendency to give a positive rheotactic reaction.

TABLE 3

Showing the quantitative daily determination of the carbon dioxide output of isopods Nos. 102 and 12. Isopod No. 12 was tested quantitatively for carbon dioxide production in the biometer; isopod No. 102, in a new apparatus especially devised for quantitative work. Column 3 gives the capacity of the respiratory chamber; column 4 shows the number of cc. of respired air which first gave the precipitate of $BaCO_3$; column 5, the amount of CO_2 given by the isopod in ten minutes, for method of calculation see page 203.

Date	Temperature in degrees C.		Volume of respiratory chamber		Minimum cc. giving Ppt. of $BaCO_3$		Amount of CO_2 given by isopods during 10 minutes in gms.	
1	2		3		4		5	
Isopod No.	12	102	12	102	12	102	12	102
Aug. 14	23	22.5	15	25	1.5	.75	10×10^{-7}	33×10^{-7}
15	23	23	15	25	1.6	.4	9.3×10^{-7}	62.5×10^{-7}
16	23.5	23.5	15	25	.55	.5	27.2×10^{-7}	50×10^{-7}
17	24.5	24	15	25	1.8	.4	12.2×10^{-7}	62.5×10^{-7}
18	24	24	15	25	1.4	2.0	10.7×10^{-7}*	12.5×10^{-7}*
19	No determination.†							
20	20.5	20	15	25	7.1	1.6	12.1×10^{-7}	15.6×10^{-7}
21	22.5	20.5	15	25	1.4	.7	10.7×10^{-7}	35.7×10^{-7}
22	22.5	22.5	15	25	.5	1.1	30×10^{-7}	22.7×10^{-7}

* Determination in some doubt due to lack of facilities for running a duplicate determination.

† No determination because of lack of carbon dioxide free air which is required n preparing the apparatus for a determination.

THE RELATION BETWEEN DAILY VARIATION IN CARBON DIOXIDE PRODUCTION AND THE RHEOTACTIC REACTION

It has been observed that the rheotactic reaction of isopods varied to a considerable degree even when the animals were kept under approximately identical external conditions. (Allee,

'13.) In order to analyze this behavior it is necessary to follow the variations in the daily metabolism which obviously cannot be done by the cyanide method because that depends on the death point of the animals. Daily determination of the carbon dioxide output of the isopods in connection with a daily test of the rheotactic reaction proved feasible. The carbon dioxide determinations were made by Tashiro in the manner already given (page 203). The rheotactic reactions were tested by Allee and neither knew the results of the other until the end of the tests. The results obtained are listed in tables 3 and 4.

From the results exhibited in table 4 it is seen that with both isopods No. 102 and No. 12 six of the seven changes of carbon dioxide production and the rheotactic response run in a parallel direction. This means that with these two isopods 86% of the variations in carbon dioxide output and rheotactic reaction were similar. The amount of variation is not always proportionate but it should be remembered that the isopods were able to move to a limited degree in the respiration chamber and that this caused an increase in the carbon dioxide production that was not controlled. Also there is a possible error of about 5% in the method of ascertaining the sign of the rheotactic reaction. (Allee, '12.) In view of these considerations the experimental results are about all that could be expected and are certainly more exact than any previous observation on the correlation of the behavior of animals upon their metabolic rate or physiological state.

Incidentally the table shows an agreement in the direction of variation of carbon dioxide production and the oxygen tension in the water in which the isopods were kept in 66% of the cases. The variations in the rheotactic response and oxygen tension agree in 73% of the cases. This seems to be good evidence that all three of these factors are more or less closely related.

The evidence here presented also makes it apparent that each individual isopod has in all probability a different rate of metabolic activity from that of any other isopod, (cf. Allee, '14) and farther that it is not a fixed standard of metabolism that accompanies a high degree of positiveness in the rheotactic response but rather a relative rate. Thus on the average isopod No. 102 (length 8 mm.) gave off over twice the amount

TABLE 4

Showing the relation between daily variations in carbon dioxide production and rheotactic reactions of isopods Nos. 102 and 12. The amount of carbon dioxide given in ten minutes may be obtained in grams by multiplying the numbers given in the second column by 10^{-7}. In the third column + indicates the results are what would be expected from our present knowledge of the rheotactic reaction if there is a direct relation between the rate of positiveness in the water current and the rate of carbon dioxide production; — indicates the opposite state of affairs. Two oxygen tensions are given; the first being that from which the isopods were taken before their rheotactic test; the second represents that in which they were placed after the carbon dioxide determination. Between testings the isopods were kept in one liter Erlenmeyer flasks which were full of water and tightly corked.

ISOPOD NO. 102

Date	CO_2 produced in 10 min. See above	Expectation	Rheotactic reaction in per cent of total trials				Efficiency in current	O_2 tension before trial	O_2 tension at start of daily interval	Temperature in degrees C.
			+	—	∞	0				
Aug.										
14	33		30	40	30		2.4	1.2	2.5	19
15	62.5	+*	20	70	10		2.3	1.8	3.0	19
16	50	—‡	60	20	20		2.4	2.35	2.35	19.5
17	62.5	+	70	10	20		3.0	1.7	2.6	21.5
18	12.5	+	40	40	20		3.0	2.5	1.9	20.5
19	....†				10	90	0.1	0.0	1.0	21
20	15.6	+		10	60	30	0.8	0.0	5.+	20
21	35.7	+	60	40			2.5	5.4	5.4	20
22	22.7	+	50	40	10		2.1	4.4	4.4	22.5

ISOPOD NO. 12

Date	CO_2 produced in 10 min. See above	Expectation	+	—	∞	0	Efficiency in current	O_2 tension before trial	O_2 tension at start of daily interval	Temperature in degrees C.
Aug.										
14	10		100				2.4	0.6	2.5	20
15	9.3	+	50	30	20		2.2	2.23	3.0	20
16	27.2	+	60	10	30		2.6	2.79	2.79	21.5
17	12.3	—‡	90		10		2.5	2.0	2.6	21.5
18	10.7	+	60	10	30		2.4	1.9	1.9	20.5
19	....†				90	10	1.3	0.0	1.0	20
20	2.1	+				100	0.0	0.0	5.+	20
21	10.7	+	50	30	20		1.45	5.4	5.4	20
22	30.0	+	70	10	20		2.0	4.4	4.4	22.5

* The increase in negativeness and decrease in indefiniteness indicate an increased rate of metabolism. (Allee, '14);

† No determination due to technical difficulties with the apparatus; carbon dioxide production in all probability very low.

‡ More work is needed before an explanation of these results can be offered.

of carbon dioxide per ten minute respiration period than did No. 12 (length 7 mm.). After making all due allowance for the effect of the slight size difference No. 102 had the higher metabolic activity yet the average percentage of positive rheotactic reactions was lower than with No. 12. Also the pair of isopods Nos. 86 and 87 (table 1, page 206) gave identical rheotactic responses but the carbon dioxide production and resistance to potassium cyanide both indicate a difference in the metabolic activity of the two animals. The same is true of isopods 90 and 91.

So far as the facts at present are known it appears that the relation between metabolic activity and the rheotactic reaction of isopods is as follows: When the metabolism of an isopod is rapid for that individual it tends to go positive to a water current, when less rapid, negative, when still less rapid, indefinite, and when least rapid, no reaction at all is given. But a rate of metabolism that is rapid for one isopod may be slow for another, and intermediate for a third. Also an individual may give identical rheotactic responses at times when its metabolic activities measured by an absolute scale vary widely. Thus isopods kept under favorable conditions including a high oxygen tension come to have a normal mean metabolic rate and also a normal mean rheotactic response. When the metabolic rate goes above its mean the rheotactic reaction tends to become more positive; when below, less positive. Put the same isopod under similar conditions except that the oxygen tension is low and the metabolic rate is depressed and the positiveness of the rheotactic reaction also decreases. But in time the isopod becomes acclimated to the new conditions and the rheotactic reaction may go up to about its old average (table 4, isopod 12, reaction for 8/14) and plays up and down as the metabolic rate changes about its new mean. So the rheotactic reaction is an expression, not of the absolute metabolic rate of the animal but of the relative metabolic rate to which the isopod is acclimated for the time being.

SUMMARY

1. The resistance of isopods to relatively strong solutions of potassium cyanide has an inverse relation to their carbon dioxide production; the higher the rate of carbon dioxide production,

the shorter the survival time in the cyanide, hence the resistance of isopods to potassium cyanide is a fair measure of their metabolic activity (page 207).

2. The calcium ion decreases the carbon dioxide production in the isopods and renders them less positive in their rheotactic reactions (page 209).

3. There is a high degree of similarity between the variation of carbon dioxide production of individual isopods and their rheotactic reaction (page 211).

4. The rheotactic reaction is an expression of the relative metabolic activity of the animal under the conditions to which it is acclimated for the time being.

January, 1914.

LITERATURE CITED

Allee, W. C. 1912. An experimental analysis of the relation between physiological states and rheotaxis in Isopoda. *Jour. Exp. Zool.*, vol. 13, pp. 269-344.

1913. Further studies on physiological states and rheotaxis in Isopoda. *Ibid.*, vol. 15, pp. 257-295.

1914. Certain relations between rheotaxis and resistance to potassium cyanide in Isopoda. *Ibid.*, vol. 16, no. 3.

Child, C. M. 1913. Studies on the dynamics of morphogenesis and inheritance in experimental reproduction. V. The relation between resistance to depressing agents and the rate of metabolism in Planaria dorotocephala and its value as a method of investigation. *Ibid.*, vol. 14, pp. 153-206.

1913a. Certain dynamic factors in experimental reproduction and their significance for problems of reproduction and development. *Arch. Entw. Mech.*, Bd. 35, pp. 598-641.

Tashiro, Shiro 1913. Carbon dioxide production from nerve fibers when resting and when stimulated; a contribution to the chemical basis of irritability. *Amer. Jour. Physiol.*, vol. 32, pp. 107-136.

1913a. A new method and apparatus for the estimation of exceedingly minute quantities of carbon dioxide. *Ibid.*, vol. 32, pp. 137-145.

1914. Carbon dioxide apparatus III. Another special apparatus for the estimation of exceedingly minute quantities of carbon dioxide. *Jour. Biochem.*, vol. 16, pp. 485-494.

THE AUDITORY SENSITIVITY OF THE WHITE RAT

WALTER S. HUNTER
The University of Texas

(One Figure)

The following is a report upon some studies of the auditory sensitivity of the white rat which are in progress at the psychology laboratory of the University of Texas. In January, 1913, tests were begun upon the discrimination of noise and tone in order to ascertain whether for the rat these are sensed as different. The discrimination box was T shaped. (See figure 1.) The

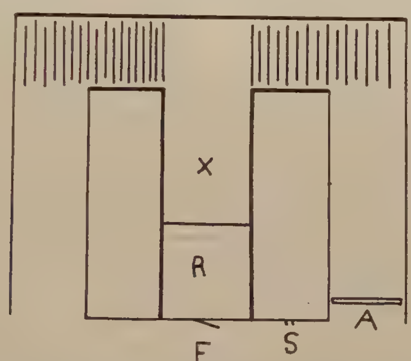

FIGURE 1. T-shaped discrimination box. F, food; R, release box; X, tuning fork was held above this point; A, alley stop, can be placed in either alley; S, switches.

animal was started at the base of the T and was required to turn either to the left or to the right depending upon the stimulus given. The source of the tone was a tuning fork held in a clamp above the apparatus and actuated by striking with a rubber hammer. The fork support was mounted independent of the apparatus box so that mechanical jars could pass through the floor only, if at all. The experimenter was prepared to introduce electric tandem driven forks, but this was found unnecessary.[1]

[1] In order to make it difficult to use the thud of striking the fork as a cue, the fork was struck just as the rat was placed in the release box. In order to make the control more sure, the fork may be actuated even sooner. While in crucial cases, this method cannot supersede the tandem driven forks, in the average case it may render the use of such apparatus unnecessary.

In order to make sure that the animal got the full benefit of the stimulus, the opening of the resonance box was directed downward upon the apparatus at a height of 19 inches. The noises were given just behind and slightly above the discrimination box. Each stimulus was given from the time the rat entered the box until the food was reached behind the base of the T. Punishment and reward were used with all of the rats. Because of the noise, the inductorium was placed in a distant room of the laboratory.

The six rats of set one were required to associate a turning to the right with the tone (c′ 512 v. s.), one trial, and a turning to the left with the noise (hand clapping), a second trial. These stimuli were as nearly equal in intensity as the experimenter could secure. The intensity of the tone was approximately equal to that of a tone produced by dropping a solid rubber ball of 102 gm. upon a rigidly held c′ 512 tuning fork from a height of 100 cm. This gives a good medium intensity. In view of the rat's poor sensitivity to intensity differences in tone (see below), these measurements are only intended to give the reader a fair notion of the intensity values employed. Five trials daily were given. All six rats learned the discrimination in from 310 to 520 trials. *All of the records show a gradual decrease in the number of errors.* Controls were instituted which indicated that the auditory stimuli alone, and not extraneous cues from the experimenter or cues from the order of presentation,[2] were determining the reactions. Two series of tests were then used: (1) The tone was withheld so that the rats received at one trial a noise and at the next trial not tone, but the absence of tone.

---

[2] When the rat is confronted with a difficult discrimination, only the greatest care will prevent the "learning of the problem" on the basis of position factors. These kinaesthetic cues are often of great complexity and are influenced by punishment. The subject will repay careful study. The following types of cases, of which some have been previously described, were noted in the present tests: (1) The rat may form a habit of going always to one side. Every day he will begin in this wise; but after a series of punishments, he may change and go to the opposite side for the rest of that day. (2) A rat may alternate between sides in the order right-left. If this leads to severe punishment, he may at times reverse the alternation to a left-right order. (3) Rat No. 5 formed a habit of alternating after *each success only*. He would go to the right and, if successful, would go to the left in the next trial. Had he failed on the right, though, he would have continued to go there until he succeeded. He would then have gone to the left where the same type of performance would be again gone through.

Behavior of this nature may give the appearance of true discrimination of the stimuli presented by the experimenter. It can only be checked up by most carefully chosen variations in the order of presentations.

Result—the reactions remained at a normal accuracy. In other words, the presence of the tone was not essential for correct reactions. (2) The noise was withheld and tone given at one trial and the absence of noise at the next. Result—the rats failed. The rat always turned to the left for the noise. It turned to the right for each of the following: tone, the absence of tone, and the absence of noise.

Two interpretations[3] were now possible: (1) The rats may be unable to hear c′ 512 either because of a shortening of the scale similar to the probable shortening of the rat color spectrum, or because of an inability to hear tone at all, i. e., complete tonal deafness, or because of a tonal island. In either of the three cases, we have a sensory defect. Furthermore, it would be a defect common to all of the rats tested. (2) The ignoring of c′ 512 may be due to a factor of attention as Dr. Weidensall has pointed out in her report at the American Psychological Association. 1912.[4] Our dilemma here is the same as the one which confronted the Watsons,[5] e.g., when their rodents were shown to be ignoring red in the red-green discrimination. The solution in either case must come from evidence drawn from tests made on mere sensitivity, i.e., the discrimination of a stimulus from its absence. In view of this the following tests were made.

Three of the rats of set one, were each given 10 trials daily, in an attempt to set up an association between the tone and turning to the right and between absence of tone and turning to the left. 410, 520 and 350 trials were given, but the association was never set up. These three rats had formed the original discrimination of noise vs. tone in 310, 370 and 520 trials respectively. In all save the third rat, therefore, the original discrimination was set up in fewer trials than given in this control. I have not regarded this as entirely conclusive, however, because as a result of previous training the rats were all ignoring the tone. This habit (if habit it were) may have persisted. A new set

[3] There is a third possibility, viz.: the rats may have been unable to discriminate the tone from its auditory background. It was impossible to carry out the tests in a sound-proof room, so this possibilitiy has not been rigorously excluded. However, the rats were accustomed to what auditory stimuli did occur, and as far as the experimenter was concerned, the tone dominated over all other sounds save in exceptional cases that rarely occurred.

[4] Weidensall, Jean. A Critique of the Discrimination Test. *Psych. Bull.*, 1912, **9**, pp. 57–58.

[5] Watson, J. B. and Watson, Mary I. A Study of the Responses of Rodents to Monochromatic Light. *Jour. Animal Behavior*, 1913, **3**, pp. 1–14.

(II) of six untrained rats was now chosen. To this group was added one rat from set I, not included in the above three. These seven rats were given ten trials daily. Table I gives the results. Not only did these rats not learn to discriminate the tone from its absence, but the data indicate that they reacted as poorly at the close of the 700 tests as at the beginning. The objection may be made that the number of trials was insufficient ! Such a criticism I should regard as valid only if the animals were slowly improving in accuracy. This was not the case. Particular attention should be drawn to the case of Rat No. 5. This rat had learned to discriminate " noise from tone " within 400 trials. The above table shows that when tested on mere sensitivity to the tone, there was no improvement in accuracy even at the end of 700 trials.

TABLE I.

The learning processes of the rats of set 11. The numbers stand for the trials in each successive fifty that were correct.

Trials	Rats						
	5	13	14	15	16	17	18
50	24	26	22	19	22	22	23
100	27	17	25	22	27	27	28
150	28	24	21	17	24	24	27
200	34	26	24	24	24	28	26
250	30	24	22	25	23	30	25
300	25	24	29	26	27	25	27
350	28	23	24	23	28	26	27
400	31	23	27	21	18	22	28
450	25	26	25	22	25	24	28
500	28	23	25	27	21	25	19
550	24	19	28	24	23	22	22
600	28	23	22	25	27	25	23
650	30	24	25	23	24	28	24
700	26	21	26	25	26	24	24

The present work is of interest when compared with that of Johnson on pitch discrimination in dogs. At the present writing his complete results have not appeared; but the preliminary report[6] shows that the dogs could not discriminate between middle C and the E above. The possibility that the dogs cannot hear these tones is not considered, although the data are in harmony with such a view.

[6] Johnson, H. M., " Some Experiments on Pitch-Discrimination in Dogs." *Psych. Bull.*, 1912, **9**, p. 59.

Comparative psychologists are agreed, I believe, that, with the higher animals, the ability to associate a stimulus with a simple response shall be the criterion of sensitivity to that stimulus. Exceptional cases may occur, as is suggested by the studies of Yerkes upon the hearing of the frog.[7] Other factors being equal, however, where an animal can learn an association with one auditory or visual stimulus, inability to do so with another auditory or visual stimulus is to be taken as evidence of lack of sensitivity. Granting this, the above data prove either that *the rats cannot hear c′* 512, under the conditions of the present experiment, or (note 3 has some reference here) that *their sensitivity is extremely slight*. The analogies between the present conclusion and that reached by other students with respect to color vision in animals are both striking and instructive. It is to be noted in particular that tone and color correspond to periodic vibrations and that noise and the white-black series correspond in general to heterogeneous vibrations. The ability to react to periodic ether vibrations is apparently a late acquisition in animals. Why then not expect, a priori, the same to be true in sound, particularly when periodic vibrations seem to be more artificial and hence rarer (at least in the habitats of non-musical animals) than heterogeneous ones? Further comment upon this must await a later presentation of data.

In addition to the above crucial evidence on the sensitivity of the white rat to c′ 512, much other material bearing upon the same problem has been accumulated. All of this, while not in and of itself decisive, is in harmony with the conclusion above drawn.

(1) All rats of set I ignored the tone and reacted on the basis of noise and the absence of noise. There must be, then, some fundamental difference in the effect of noise and tone on the rat. Otherwise we should expect individual differences to appear.

(2) Six rats of an untrained set (III) all failed to discriminate a very intense sounding of c′ from a faint sounding of the same tone. These two intensities may be described with sufficient accuracy as follows: One was as intense as could be secured by striking the fork. The other was approximately of

[7] Yerkes, R. M. "The Sense of Hearing in Frogs." *Jour. Comp. Neur. and Psych.*, 1905, **15**, pp. 279-304.

the same intensity as a tone produced by a solid rubber ball of 102 gm. striking the fork after a free fall of 25 cm.

The conditions of testing here were the same as described above. Five trials daily were given, save at certain periods with two rats, with punishment and reward. Between 575 and 800 trials were given. There was no more evidence of discrimination at the last than at the first. This problem of intensity discrimination was begun simultaneously with the work on noise and tone before I suspicioned that the rats were insensitive (or very slightly so) to the tone in question.

(3) Miss Alda Barber of this laboratory is studying localization of sounds in rats. The standard stimulus, tapping upon wood, is well localized. The following controls have been used with significant results: (a) Tapping with the rubber end of a lead pencil on the resonance box of c′ is localized with normal accuracy. This gives a noise predominately of a 512 v. s. pitch. (b) A tuning fork c′ sounded steadily is completely ignored. (c) The same pitch blown upon an organ pipe as an interrupted (tooting) tone is also ignored. It is not known yet whether or not special training will overcome these last two failures.

(4) Watson[8] obtained reactions from white rats with the Galton whistle. I have never secured an *unambiguous* response to tone, although violent starts are often made to the *slightest* noises. A few times I have thought that reactions occurred. These may well have been to the noise accompanying the whistle tone. Tests have been made with organ pipes and Edelmann-Galton whistles. At least 30 rats have been tested in this laboratory both when they were awake and when they were asleep, when they were nervous and responded to slight noises readily and when they were not nervous. A few tests were made upon some twenty rats at the University of Chicago in the summer of 1913. The Edelmann whistle was used throughout its range, but no reactions were observed. Professor R. E. Carter of the University of Kansas witnessed these latter tests and agreed in the findings. Possibly it is true that rats are sensitive to each others squeaks, but who is to say whether these are more tone than noise?

This type of test is to be carried further. At present this

[8] Watson, Jno. B. "Kinaesthetic and Organic Sensations." *Psych. Rev. Mon.*, 1907, 8, pp. 53-54.

method of "general response" has convinced me more strongly merely that there is a fundamental difference for the rat in noise and tone.

(5) It will be recalled that only three rats of set I were tested immediately upon sensitivity to tone vs. no-tone. The other three rats were tested as follows: In place of hand claps, the following noises were each substituted for five trials from time to time: (a) rattling of paper; (b) dropping sunflower seed on tin; (c) scratching on wood; (d) drumming on the table with the fingers; (e) rubbing two pieces of board together; (f) hissing through the teeth; and (g) rattling of nails in a glass. Pitch, volume and quality varied greatly, but a rough attempt was made to keep the intensity values equal to that of the tone. (See above, page 216.) *The rats responded to all of these stimuli as accurately as to the regular stimulus of hand claps*, i.e., never below 80% correct. Rat No. 5 failed to react correctly to noises e and f, i.e., although repeatedly tested, he never made more than from 55% to (at most) 70% correct. This was the rat tested later with set II, on tone vs. no-tone, with negative results. In view of those tests, his failure to respond correctly to the two noises is to be explained on the basis of their dissimilarity to the standard noise rather than upon their likeness to c′ 512, which tone this rat seems not to hear.

Tests were also made in which each of the following tones were substituted for the original c′ on the fork on enough occasions to be sure that the reactions were not due to chance: (1) c‴ 2048 on the fork; (2) c′ 512 v. s. on the organ pipe, sounded steadily; (3) No. 2, sounded interruptedly, i.e., in toots; (4) c″ 1024 on the organ pipe, sounded steadily; (5) No. 4 sounded interruptedly; and (6) f 341.3 on the organ pipe, sounded steadily. With *no exception*, the rats reacted to these tonal stimuli as to the original tone which had been sounded steadily, i.e., they ignored them. There are many suggestions as to interpretation which arise from these results. The points that can be definitely stated are these: (1) All of the tones given were for some reason very different from the noises. (2) This difference was not the fact of smoothness, i.e., lack of interruptedness. This point seems conclusively proved, because on the same day with the interrupted noises were given trials with the interrupted tones, yet the rats paid no more attention to

the tones than if they had been continuously sounded. Inasmuch as the animals reacted in the same manner to all of the noises, it is certainly a striking fact that none of the tonal stimuli given were classed as noises. Further experimentation alone will determine whether sensory defect is the reason for neglecting all of the tones given here. Such an explanation certainly seems necessary for the lack of sensitivity to c′ 512.[9]

At the present, the above work is being extended in three directions: (1) Search is being made throughout the pitch scale for a tone to which the rats will respond. Both continuous and interrupted tones will be used. When an effective tone is found, the original problem will again confront us, viz., can rats hear noise and tone as distinct experiences. (2) Miss Barber's work will probably throw added light upon the question of relative sensitivity to noise and tone. (3) Mr. A. C. Scott is beginning tests which are expected to emphasize the relations between vision and hearing with respect to the learning processes involved. One problem with which he will deal will be this: Is the simultaneous presentation of stimuli, such as is used in visual discrimination, more favorable to learning than a successive presentation of stimuli, such as must be used in auditory discrimination work?

One additional matter needs comment. So far as I have been able to ascertain there are no published studies on the anatomy of the white rat's ear. I am supported in this statement by several eminent authorities. In view of the results above presented, it is at least possible that careful anatomical studies might throw light upon the structural basis for the perception of noise and tone.

---

[9] Johnson's work[10] has appeared since this paper went to press. On pp. 44–45, the author reports negative results at the conclusion of 150 trials on mere sensitivity to a tuning fork of 256 d. v. The suggestion is made from this that in ordinary noises the dog may reach only to high overtones.

[10] Johnson, H. M. Audition and Habit Formation in the Dog. Behavior Monographs, **2**, no. 3, 1912.

BEHAVIOR OF THE MEDITERRANEAN FRUIT FLY (*CERATITIS CAPITATA* WIED.) TOWARDS KEROSENE

HENRY H. P. SEVERIN, Ph.D. and HARRY C. SEVERIN, M.A.

The following observations on the behavior of the Mediterranean fruit fly toward kerosene were made in the field in Manoa Valley, situated on the outskirts of the city of Honolulu, Hawaii. On account of the abundance of rainfall in this valley, the kerosene traps used in our experiments consisted of pans three and one-half inches in depth and twelve inches in diameter. Each pan was wired to the lower branches of a fruit tree (Fig. 1).

FIGURE 1. Pan containing kerosene wired to the lower branches of a fruit tree, to trap the Mediterranean fruit fly.

Enough kerosene was poured into each pan to cover the bottom so that in case of a heavy rain, the kerosene might overflow directly to the ground and not injure the tree. After a light or moderate rain such traps are probably just as effective as when there is no precipitation, for the oil floats on the surface of the water.

The first problem which presented itself was to determine whether the color of the pan containing the kerosene made any

difference in the number of Mediterranean fruit flies caught. Five white, three black, one blue and seven orange-colored pans were wired to the branches of orange, lemon, grapefruit and guava trees. From the results of our catches in the various pans, it was evident that the number of fruit flies captured was not influenced by the color of the pans. Moreover, it is highly probable that the sense of smell is the determining factor in attracting these insects to the kerosene.

In our second experiment we endeavored to ascertain in what particular kind of fruit-bearing tree of an orchard the pest would be captured in largest numbers with the kerosene traps. Accordingly, one pan was wired to the lower branches of a common guave tree (Psidium guayava pomiferum), nine pans were fastened in nine different navel orange trees (Citrus aurantium), and one pan was placed in a Java plum tree (Syzygium jambolana). All of the pans used in this experiment were enameled white, because most insects caught in the oil were more conspicuous against such a background. The following table shows the number of fruit flies taken at intervals of three to four days for a period of eighteen days in the kerosene traps attached to the three different kinds of fruit trees:

TABLE 1

NUMBER OF MEDITERRANEAN FRUIT FLIES CAPTURED IN KEROSENE TRAPS PLACED IN GUAVA, ORANGE AND PLUM TREES.

	Trees		
	One guava	Nine navel orange	One Java plum
Four days catch	75	1155	398
Four days catch	33	749	207
Three days catch	25	715	213
Three days catch	16	422	60
Four days catch	35	1093	295
Eighteen days catch	184	4134	1173
Average capture per day in 1 trap	10	25	65
Total number of males captured			5461
Total number of females captured			30
			5491

It is evident from this table that the attraction of the Mediterranean fruit fly to the kerosene was confined almost entirely to the male sex. Female flies were present in this orchard because hundreds were caught by sweeping with an insect net among the fruit trees. Trapping the pest with kerosene was carried on for a period of eight months in the Hawaiian Islands in connection with other experiments and the results show that of every one thousand fruit flies captured only three on an average were females, the remainder being males.

A dissection of some of the flies captured in the kerosene trap wired to the Java plum tree showed that the alimentary canal was filled with the blue juices of the plum. The ripe plums were seriously infested by the maggots of different species of Drosophilidae and the juices were exuding from the punctured and bruised fruit. Mediterranean fruit flies and some of these plums were placed in a breeding jar and frequently the Trypetids were seen feeding on the plum juices. The reason why more specimens were captured in the kerosene trap wired to the Java plum tree finds its probable explanation in the fact that the plum is more attractive to the pest then the common guava or navel orange, or possibly because the plum juice was more available than the juices of the less bruised guavas and oranges.

The Mediterranean fruit fly was often captured in kerosene traps wired to trees that were not bearing fruit and also near fruits in which the pest has not been reported to breed. Kerosene traps were fastened repeatedly in mango trees (Mangifera indica) months before the mango season was on, and in every instance fruit flies were trapped. One trap was wired in an isolated bread fruit tree (Artocarpus incisa) which at that time bore very hard, green fruit, and in four days twenty-nine male Mediterranean fruit flies were caught. A kerosene trap was also placed in a clump of mulberry shrubs (Morus nigra) bearing ripe fruit, and in four days twelve male flies were taken. In the last catch the flies may have been attracted by the ripe fruit, the juices probably serving as food material for the adults. The interesting part of the last two catches rests in the fact that the pest under consideration does not breed in the fruits of these trees.

In all probability the reaction of the male Mediterranean

fruit fly to kerosene is not in any way connected with the feeding habits, but too much emphasis, however, should not be attributed to any of these experiments, for the distance that kerosene will attract the flies is not known.

Weinland (2, page 847) claims that the sphere of influence of kerosene " is limited, being possibly fifty feet or so, varying with the wind, freshness of kerosene, etc." Howlett (1, page 414) of India says the distance at which the fruit flies (Dacus zonatus Saund.) are able to perceive the smell of citronella oil "is doubtful, but seems to be considerable; half a mile is probably not extravagant an estimate if the wind is favorable."

The behavior of the Mediterranean fruit flies was occasionally observed in the neighborhood of the kerosene traps. In some instances fruit flies remained at rest on the inside of the pans for long periods of time as if stupefied by the volatile parts of the oil. In other cases, the flies would walk along the inside of the pan for a time, then take wing and fly up to a neighboring leaf or twig, or in their apparently dizzy, zigzag flight over the surface of the oil they would plunge into the kerosene and generally cease all activity noticeable to the naked eye in less than half a minute.

It certainly is peculiar that the Mediterranean fruit fly plunges into the kerosene to its own destruction. The flies may be attracted to the oil as a result of a chemotaxis due to one or more hydro-carbons or to the impurities of the petroleum oils, such as the sulphur constituents or nitrogenous products. Small quantities of sulphides are detected by the human nose and it may be possible that the minutest traces are perceived by the fruit flies. Furthermore, sulphides have recently been found within the bodies of insects. Again, the hydro-carbons of the oil may act as an anesthetic, and stupefy the insects whenever they remain within its influence. It is known that the volatile parts of gasoline, for instance, have a stupefying effect upon animals. According to a scientist connected with the Standard Oil Company, cases are on record where men, who had opened barrels of gasoline, were suddenly overcome by the fumes and plunged "head-first" into the oil. Large gasoline tanks which have been recently emptied are dangerous for men to go into, and require about twenty-four hours of ventilation before they are safe for a human being to enter.

Why should enormous numbers of male fruit flies and only a few females be captured in certain oils? Concerning the behavior of Dacus zonatus towards citronella oil, Howlett (1, page 413) writes: " Since the reaction was confined to the male sex and did not appear to be in any way connected with feeding habits, it seemed most reasonable to suppose that the smell might resemble some sexual odour of the female which in natural conditions served to guide the male to her." This is, in substance, a view which we also expressed to a number of entomologists and mentioned in a paper read before the Agricultural Seminar in Honolulu on January 11, 1912, to explain the behavior of the male Mediterranean fruit fly towards kerosene. Howlett believes that "the smell is in all probability perceived by means of the antennae," for, after he had carefully amputated these "at the base of the second joint," none of the mutilated insects were attracted to the oil of citronella.

If it is true that kerosene gives off an odor which resembles that emitted by the female fruit flies to attract the opposite sex, then how would the fact be explained that a few females are usually caught in the oil? We would have to assume that the specialized sense organs present in the males to locate the females are absent in the latter. We would then be forced to conclude that the females were not attracted to the kerosene, but came within the sphere of influence of the oil by accident, became stupified and dropped into the oil. There is, of course, the possibility that the reaction of the male Mediterranean fruit fly towards some volatile part of the petroleum oils may be a positive chemotaxis "not representing the sexual smell of the female," a possibility to which Howlett also calls attention in the behavior of Dacus zonatus toward citronella oil.

BIBLIOGRAPHY

1. Howlett, F. H. The Effect of Oil of Citronella on Two Species of Dacus. 1912. *Trans. Ent. Soc. London*, pt. II, pp. 412-8.
2. Weinland, H. A. The Present Fruit Fly Situation and some Results of the 1912. Hawaiian Campaign. *Cal. State Comm. Hort.*, Mon. Bull. I, No. 11, pp. 845-852.